DEMOGRAPHICS OF A SEASONAL AGGREGATION OF WHITE SHARKS AT SEAL ISLAND, FALSE BAY, SOUTH AFRICA

Adrian Michael Hewitt

Dissertation presented for the degree of Master of Science

Department of Biological Sciences, University of Cape Town,

South Africa

May 2014

Supervisors:

Prof. Charles Griffiths

Prof. Tony Booth

Alison Kock

DECLARATION

I hereby declare that all of the work in this dissertation is my own, except where otherwise stated in the text. This thesis has not been submitted in whole or in part for a degree at any other university.

Signed by candidate

Adrian Michael Hewitt

28 May 2014

TABLE OF CONTENTS

ACKNOWLEDGEMENTS

First and foremost I acknowledge my appreciation for everything that Alison Kock has done for this project since 2004, and for me personally since we have been a research team. Specifically, I thank Alison for her unwavering support and sound advice, for providing the opportunity to collect data in False Bay personally (2009-2012), and for the supply of photographic material and data (2004-2012) used in this study. I would like to personally thank Morne Hardenberg, not only for his loan of a computer at such a crucial time, but also for his logistical expertise, time and effort, which has assisted tremendously over the years with collection of data and the logistics of running white shark field operations. I extend my sincerest gratitude to Professor Tony Booth for his dedication, patience, time and advice during project development, and especially for his willingness to accommodate and support this project; also for sharing his extensive insight into population modelling and particularly for his efforts with manuscript structure, development and editing. I thank Professor Charles Griffiths and Alison Kock for their advice, guidance and support (academic and financial), throughout this long degree, and for their assistance with manuscript editing.

I acknowledge and extend my sincerest gratitude to the multiple financiers whom have supported this project over the years (Save Our Seas Foundation, Shark Spotters and the City of Cape Town), but also to those that have financed my personal studies; specifically, Prof. Coleen Moloney (Marine Biology Research Centre Bursary, 2010), Prof. Charles Griffiths and Prof. Tony Booth (student bursary 2013), the University of Cape Town Postgraduate Centre and Funding Office (student bursary 2010), and the National Research Foundation (DST Innovation scholarship 2011). I further extend my sincerest thanks to the Department of Ichthyology Fish and Fisheries, Rhodes University, for their much appreciated hospitality during my extended stay in Grahamstown. I further acknowledge assistance from Oceans Research and specifically Rabia Ryklief and Ryan Johnson for providing a suitable framework from which to develop the photo-identification catalogue in Adobe Lightroom. I extend my gratitude further to Timo Seckler and to all of the other research assistants, interns and helping hands, who have collected data and photographs over the years. I would like to thank the two anonymous examiners for their time and suggested improvements to the final version of this dissertation. Finally, a huge thank you to my parents, Anne and John, my brother, Alex, and family, and my love, Kari Underhill, for everything over the years and of late! Without everything you have done for me none of this would have been possible!

DEDICATION

To white shark WS0001 and the sharks of southern Africa, live long and prosper...

"White shark dorsal fins are similar to human faces, they are unique to each individual, and whilst both might change slightly with age, acquiring pigment spots, creases and wrinkles, their basic structure can be used to differentiate among individual's, typically from birth to death for the bulk of the population".

ABSTRACT

White sharks (*Carcharodon carcharias*) are widely distributed, ecologically important marine apex predators that are considered to be vulnerable to extinction. Given their crucial roles in structuring marine ecosystems", their populations need to be effectively monitored. Photo-identification provides a standardised, non-lethal method of assessing the population dynamics of extant species and provides live-encounter mark-recapture data that are essential for management and conservation. White sharks occur throughout South African coastal waters but their centre of abundance is the Western Cape, where large sharks predominate at aggregation sites like Seal Island, False Bay. This study documents inter- and intra-seasonal trends in mean sighting rates and sex ratios of white sharks at Seal Island, and provides mark-recapture data that are used to estimate proportions of „resident" and „transient" white sharks, their size-distribution and maturity composition. A total of 1105 sightings were recorded (sex ratio 1.0: 1.0: 2.3, male–♂: female–♀: unsexed–*U*) over the 34-month sampling period June 2004–September 2012. The mean annual sighting rate was 1.87 sharks per hour, and sighting rates decreased significantly over the nine-year study period. Of the 1105 sightings, 39% were photo-identified, representing 303 uniquely marked individuals (112: 111: 80, ♂: ♀: *U*). Of these, 71% were transients that were never recaptured, whereas 29% were repeat visitors, termed residents, recaptured in at least one other year, 98% of which were recaptured in <3 years. Of the residents, 65% were recaptured the following year, indicative of short-term fidelity to Seal Island, whereas 35% skipped one or more years between encounters, indicative of temporary emigration. The most common size class was 300–349 cm (range 170–550 cm), and 60% of sampled individuals were immature, 32% sub-adult, and 8% mature. Large females dispersed when they approached maturity (>450 cm), while certain males were recorded consistently across years as adults, supporting that Seal Island is a critical area for large, maturing white sharks. Live-encounter mark-recapture data for the 303 different white sharks were used to estimate probabilities of capture (p), apparent survival (ϕ) and permanent entry of new individuals into the population (β), as well as annual and super-population sizes (N), using the POPAN formulation of the Jolly Seber (JS) model. Capture probability (p) was highest in 2004–2006, lowest in 2007–2009 and was most variable in 2010–2012. Male–p increased and was greater than for both female and unsexed sharks in 2010–2012, which both remained low and constant from 2007 onwards, providing evidence to support the notion that female"s permanently emigrated from the population. Estimates of apparent survival fluctuated across years between clustered 2–3 year periods, but showed no trend over time or variation among sexes. The probability of new sharks entering into the population (β) gradually increased each year in 2004–2008 and persisted at relatively low and consistent levels throughout the study, except in 2009, when it peaked, with the recruitment of many newly captured individuals. General trends in abundance reflected variation in β estimates with a similar peak in 2009, which persisted into 2010. Annual population sizes decreased in 2011 and 2012 for males, females and unsexed sharks, despite sampling effort being highest, most persistent and proficient in later years. Respective super-population size estimates for male, female and unsexed sharks were 204 ± 22 SE, 223 ± 30 SE, and 297 ± 80 SE individuals, and the superpopulation size for Seal Island was 723 ± 132 SE individuals, with a range of 12–287 individuals estimated to be present in any year. The permanent emigration of large females approaching size-at-maturity (450 cm total length) detected across several analyses in this study, and the absence of mature and pregnant females at other South African sites, emphasises that the reproductive habitats of white sharks in the region remain poorly understood. Building on previous research, the findings in this study present an opportunity to propose a first life history hypothesis for the western Indian Ocean white shark stock.

CHAPTER 1

GENERAL INTRODUCTION

INTRODUCTION

Anthropogenic impacts on species and ecosystems have expanded globally at alarming rates (Willson *et al*., 2011). This fact is highlighted by the current rate of biodiversity loss that is several orders of magnitude greater than the background extinction rate (Baillie *et al*., 2004; Mace *et al*., 2005). Worldwide, multiple studies have shown that human removal of top predator species from all major ecosystems has resulted in extensive cascading effects, that are both unpredictable in nature and extremely devastating (Estes *et al*., 2011). Thus, recognition has grown of the need to monitor wildlife populations to ensure sustainability of biodiversity (Willson *et al*., 2011).

In marine ecosystems, sharks are among the top predators that perform important regulatory roles integral to their structure and correct functioning (Bascompte *et al*., 2005; Heithaus *et al*., 2008); a process mediated through direct and indirect predatory effects (Stevens *et al*., 2000; Heithaus *et al*., 2002, 2008), which maintain biodiversity by regulating genetic fitness of prey (Zoo, 2004). Concerns have increased in recent decades over the conservation of sharks (FAO, 1999), as their removal can have disastrous effects on marine ecosystems and biodiversity integrity (Stevens *et al*., 2000; Ward and Myers, 2005; Myers *et al*., 2007; Dulvy *et al*., 2008; Heithaus *et al*., 2008).

Vital demographic data are deficient for many species, which are, however, generally known to be long-lived, large-bodied and slow-growing. Consequently, they mature late in life and produce few young, which results in slow population growth rates and low rebound potentials. Once stocks are depleted populations thus struggle to recover, rendering sharks highly susceptible to over-exploitation (Dulvy *et al*., 2008). Many shark species have been exploited in recent decades (Baum *et al*., 2003; Baum and Myers, 2004), both as bycatch in pelagic long-line fisheries (Bonfil, 1994) and in directed shark-finning fisheries (Rose, 1996).

Worldwide, a conservative 100,000,000 sharks are killed annually (range 63–273 million; Worm *et al*., 2013), targeted primarily for their valuable fins in the wasteful, unsustainable fishing practice known as finning. This lucrative trade exists solely to supply the demand for shark fin soup, considered by some in the Far East to be a traditional delicacy

(Clarke *et al*., 2007; Dulvy *et al*., 2008). Consequently, many sharks are faced with extinction in the near term future, with significant declines reported from many areas globally, especially for pelagic elasmobranchs (Dulvy *et al*., 2008). Disturbingly, this global downward trend in shark abundance shows no indication of ceasing or slowing any time soon (Worm *et al*., 2013). Even large, high profile species, such as white sharks (Figure 1.1), are not exempt from the international trade in shark fins (Shivjy *et al*., 2005).

Figure 1.1.Adolescent female white shark finned in Guinjata Bay, Mozambique (image courtesy A. Bough, taken 22/01/2013).

White sharks - *Carcharodon carcharias*

The regional centre of abundance of *C. carcharias* encompasses the east coast of southern Africa from False Bay (F.Bay) (Figure 1.2) in the Western Cape to KwaZulu-Natal (KZN) Province on the east coast of the country (Compagno, 2001). White sharks form localized seasonal aggregations related to, but not necessarily limited to, seasonal abundance and availability of prey (Klimley, 1985; Klimley and Anderson, 1996; Ferreira and Ferreira, 1996; Strong *et al*., 1996; Kock and Johnson, 2006; Robbins and Booth, 2012; Kock *et al*., 2013). Both sexes show a high degree of site fidelity and are known to disperse widely and regularly and utilise multiple habitat types throughout their life cycle (Domeier, 2012). Reasons for these broad scale open ocean movements remain unclear, but are presumed to be related to feeding opportunities, thermal preferences, and/or reproductive behaviour (Bonfil

et al., 2005; Bruce *et al*., 2006; Bruce and Bradford, 2008; Bruce, 2009; Domeier, 2012; Domeier and Nasby-Lucas, 2012; Jorgensen *et al*., 2012; Robbins and Booth, 2012; Smale and Cliff, 2012; Semmens *et al*., 2013). Although dispersal events are known to be relatively common behaviour, they are not well understood and timing of movements differs between areas and sexes (Strong *et al*., 1996; Kock and Johnson, 2006; Domeier and Nasby-Lucas, 2008, 2012; Domeier, 2012; Nasby-Lucas and Domeier, 2012; Robbins and Booth, 2012; Kock *et al*., 2013).

Figure 1.2.Juvenile white shark (*Carcharodon carcharias*) photographed in the waters around Seal Island, False Bay, by author (2012).

Conservation status

Intense hunting in South Africa between the 1950‟s and 1980‟s led to anecdotal evidence for declines in abundance of large white sharks in the Western Cape prior to the species‟ protection in 1991 (Ferreira, T. Pers. comm. cited by Cliff *et al*., 1996a). In April 1991, the South African government adopted a precautionary approach and granted full protected status to *C. carcharias* in the country‟s exclusive economic zone (Compagno, 1991).White sharks were listed in CITES Appendix II (Convention of the International Trade in Endangered Species of Wild Fauna and Flora) in 2005 due to the species low intrinsic rate of population increase (Cailliet *et al*., 1985; Francis, 1996; Pratt, 1996) and low intrinsic density (Compagno, 2001). White sharks have since been red listed in IUCN (2011) Category A2cd+3cd ver. 3.1 and are therefore considered vulnerable to extinction in the near term future and threatened on a global scale. Encouragingly, *C. carcharias* is afforded the highest protective level of any elasmobranch (Chapman *et al*., 2003); although this decision is largely based on the precautionary approach because this species is classified as data deficient.

Threats

Despite a high level of protection globally, direct fishing pressures still exist from the commercial targeting and illegal poaching of large white sharks for their teeth, jaws and fins, sold as trophies or curios that have significant economic value (Compagno *et al.,* 1997). White sharks are killed as incidental bycatch in commercial and artisanal fisheries using long-lines, hook-and-line, gill-nets, trammel-nets, whelk-fishing hoop nets (Figure 1.3), fish-traps, herring-weirs, harpoons, bottom and pelagic trawls, as well as purse seine nets (FAO, 1999).In South Australia, Bruce (1992) and Strong *et al*. (1996) reported that 30% and 10% of white sharks, respectively showed evidence of previous encounters with commercial fishing gears(i.e. short < 2 m remnants of long-lines and gill nets). White sharks may also be destroyed intentionally when they reduce fisheries catches through depredation (Bruce, 1992; IUCN Shark Specialist Group, 1998).

Further threats that face white sharks include habitat loss and degradation and prey source deletion, pollution such as plastic debris (Cliff *et al*., 2002), boat propeller strikes (Hewitt, 2008; Towner *et al*., 2012), fatal encounters with spear fisherman (Cliff *et al*., 1996b; pers. comm. Kock, 2011), unregulated, unethical ecotourism, human interference during predatory events, and a poor public image that often leads to calls for culling after rare bite incidents (CITES, 1999; Kock *et al*., 2013). Gill-nets used by the Kwazulu-Natal Sharks

Board‟s (KZNSB) beach-meshing bather-protection program present a moderate threat to white sharks in South Africa, with catches currently considered stable (FAO, 2004). The primary function of the nets is to reduce the incidence of shark attack (Cliff *et al*., 1989), the primary mechanism for achieving this being removal of large predatory sharks (Davies, 1964; Wallet, 1973; Dudley, 1997) that present a potential, albeit minimal, threat to human life. While the nets have reduced the incidence of shark bite inflicted human mortalities (Dudley, 1997), they have also removed approximately 1000+ *C. carcharias* and many other shark and non-shark species since 1952.

Figure 1.3.A 440 cm TL subadult female white shark, incidentally captured in an experimental whelk hoop net fishery in Fish Hoek Bay, False Bay, South Africa (taken by author 11/03/2012).

In False Bay, Lamberth (2006) reported 20 juvenile white sharks taken as bycatch in the traditional beach seine fishery (1974–2006). Recreational white shark fisheries still operate in Mossel Bay (M.Bay) and F.Bay, documented by the capture of a white shark in M.Bay in 2011 (Figure 1.4) followed by prosecution of its captor in 2012. It is difficult to assess the impacts that these threats have on white shark populations. However, direct and incidental fishing pressures (commercial and recreational), public disregard for conservation measures and inadequate enforcement of protective legislation globally, all undoubtedly impact populations of this naturally rare and threatened species (Compagno *et al.,* 1997).

Figure 1.4.Fisherman posing for sport with an injured juvenile white shark caught on rod and line in Mossel Bay (image courtesy of http://metro.co.uk/2013/02/07/worlds-first-ever-conviction-over-death-of-great-white-shark-sees-fisherman-given-R8000-fine., taken 14/10/2011).

Global trends: abundance and demography

Despite its wide-ranging habits, large adult size, few natural competitors and fearsome reputation as a predator, *C. carcharias* is one of the least demographically resilient elasmobranch species (Dulvy *et al*., 2008). Several studies have reported anecdotal evidence of abundance declines in South Africa (Cliff *et al*., 1996b), Australia (Bruce, 1992; Strong *et al.,* 1992) and off the U.S. West Coast (Klimley and Anderson, 1996), although no data, nor quantitative estimates, exist for global superpopulation size (CITES, 1999). Several regions have reported negative abundance trends and rapid population declines, highlighting the need for improved knowledge of the species (Malcolm *et al*., 2001; Soldo and Jardas, 2002). Incidental catches of white sharks are reported to have declined by 79% (95% CI, 59–89%) in the Northwest Atlantic U.S. pelagic long-line fishery, with 6087 individuals landed over a 14 year period (Baum *et al*., 2003). Population status remains uncertain and, although widespread, white sharks are considered uncommon to rare (Fergusson, 1996).

Global population estimates have reportedly been hampered due to low recapture rates and/or abbreviated observation times (Cliff *et al*., 1996b; Strong *et al*., 1996). These have been attributed to the intractability of white sharks and further to the difficulties

associated with studying the population biology of a vulnerable, protected species using non-lethal methods. Few reliable techniques exist to estimate white shark abundance and other vital demographic rates, such as survival, or to measure the impacts of mortality on populations (Cailliet, 1996). Limited population trend data come from a number of sources, including beach meshing programs (Cliff *et al*., 1989, 1996a, 1996b; Reid and Krogh, 1992; Malcolm *et al*., 2001; Dudley and Simpfendorfer, 2006), game fishing captures (Casey and Pratt, 1985; Bruce, 1992; Pepperell, 1992; Presser and Allen, 1995), catch and sighting per unit effort (CPUE and SPUE) analyses (Cliff *et al*., 1996a, 1996b; Strong *et al*., 1996; Baum *et al*., 2003; Ryklief, 2012), and mark-recapture studies (Cliff *et al*., 1996b; Strong *et al*., 1996; Chapple *et al*., 2011; Sosa-Nishizaki *et al*., 2012; Nasby-Lucas and Domeier, 2012; Towner *et al*., 2013).

South Africa: population composition

White shark demography remains poorly understood in South Africa, with the majority of research having been restricted to fisheries-independent surveys conducted by the KZNSB. The Sharks Board have rigorously applied CPUE techniques to a comprehensive data set of white shark catches spanning approximately 40 years from 1978–2012 (Cliff *et al*, 1989, 1996a; Dudley and Simpfendorfer, 2006; Dudley, 2012). At present, the nets provide the only reliable long-term source of population trend information in South Africa, which is largely deficient for Southern and Western Cape aggregation sites and hence the known centre of abundance for the population (Bass *et al*, 1975).

Catch rates and trends

In KZN, Cliff *et al*. (1996a) reported catches of white sharks throughout the year, but with greatest frequency in August-January (late-winter to mid-summer), with peaks in July (mid-winter) in 1978–1988 and August (late-winter) in 1989–1993. Mean annual white shark catch was 41.0 $\pm$ 6.1 (SE) individuals between 1966 and 1972 (annual range 24-74), and 35.8 $\pm$ 2.6 (SE) individuals between 1978 and 2003 (Dudley and Simpfendorfer, 2006).

Cliff *et al*. (1996a) described two general trends in catch rates; the first was a sharp decline in1952–1972 (Wallet, 1973), attributed to a fishing-out phase and removal of the local elasmobranch community, as the trend was apparent across all species combined (Dudley and Cliff, 1993a). Catch rates have since been stable for white sharks (FAO, 2004) with available evidence indicating that the catch composition has not changed markedly in

recent decades. Dudley and Simpfendorfer (2006) suggest that the population may have increased by as much as 1.6% per annum, although this estimate should be regarded with caution, as inter-annual variability in catch rates was high (Cliff *et al*., 1996a; Dudley and Simpfendorfer, 2006; Kock and Johnson, 2006). Dudley and Simpfendorfer (2006) assessed a medium threat potential effect on the population, based on the species‟ low intrinsic rate of population increase (*r*), small population size and a moderate annual catch. This suggests that intensive fishing pressure from other regions, such as Mozambique (Figure 1.1), could be detrimental, given the population is presumed close to equilibrium at present with current fishing effort in KZN.

The second trend was marked cyclical peaks in white sharks catches every 4–6 years in 1968, 1973, 1978, 1984 and 1989, which were presumed to be the result of natural variation in abundance within the netted region, but were also linked to warm and cool phase weather pattern oscillations, El Nino and El Nina events, respectively (Cliff *et al*., 1996a). High winter catch rates were correlated with high rainfall and a low sea surface temperature (SST) during the preceding summer, as well as increased water turbidity, easterly wind flow and cold-water upwelling (Cliff *et al*., 1996a).

Size distribution and maturity composition

Dudley and Simpfendorfer (2006) reported 375 cm TL as the estimated 50% size-at-maturity for males, and approximately 475 cm TL size-at-maturity for females, approximated because no mature females have been caught in the nets since their installation in 1952 (Compagno, 2001; Francis, 1996; Dudley, 2012). Wintner and Cliff (1999) assessed vertebral growth bands and estimated size range at birth at 126–169 cm TL, and assuming annual deposition of growth rings age-at-maturity was estimated at 8–9 y for males and 16 y for females.

Between 1966 and 1972, white sharks caught in the nets were all immature (Wallet, 1973) although Wallet (1978) reported the capture of a 480 cm TL female, but presented no information on its maturity (Dudley, 2012). For the period 1978–1989, Cliff *et al*. (1989) reported mature specimens as absent, but provided modal lengths of males and females as 265–270 cm TL and 253–258 cm TL respectively. No trends were evident in the mean or median size of males, or in the median size of females, but the mean female TL significantly decreased (Dudley and Simpfendorfer, 2006). Dudley (2012) noted this was a probable consequence of sex-biased philopatry, as described by Pardini *et al*. (2001).

Between 1989 and 1993, Cliff *et al*. (1996a) documented the first catches of three mature male sharks sized 350 cm TL (1989), 384 cm TL (1992) and 452 cm TL (1992), as well as two other large immature males sized 374 cm TL (1991) and 387 cm TL (1992). White sharks > 500 cm TL, which probably include most mature females, have not been observed in shelf waters off KZN (Dudley, 2012), and although large free-swimming sharks (350–500 cm TL) have been observed at whale carcasses off Durban (Cliff *et al*., 1996a; Dudley *et al*., 2000), encounters are less frequent than at Western Cape aggregation sites. It is probable that this size class of shark (> 500 cm TL) seldom occurs in coastal waters off South Africa (Dudley, 2012).

Mark-recapture abundance estimates

In areas where attempts have been made to quantify abundance, the general consensus is that *C. carcharias* is naturally rare. Worldwide, six studies have used mark-recapture techniques and basic closed and open population models to estimate white shark population size and other demographic parameters. In South Africa, Cliff *et al*. (1996b) provided a first estimate of white shark population size off the south and east coasts, by analysing conventional tag returns from six recaptures of 73 tagged white sharks caught in the nets (supplemented with commercial and recreational fisheries catches in the Western Cape) with the „closed" Lincoln-Peterson estimator to derive a population estimate of 1279 individuals (95% CI, 839–1843). However, this study only included information for sharks encountered between Richard's Bay (KZN) and Struisbaai (WC) along the south and east coasts, and whilst data were collected across a large expanse of the South African coast in absolute terms (1,375km), key aggregation sites and sharks from significant areas of abundance were not included, specifically from G.Bay and F.Bay. Cliff *et al*. (1996b) estimated mortality rates as $F = 0.055$ year^{-1} (95% CI, 0.015–0.10) and $Z = 0.055$ year^{-1} (95% CI, 0.42–0.66), with survival constant at α 0.90, and concluded that improved estimates of mortality are needed before relaxation of protective legislation could be considered.

More recently in South Africa, Ryklief (2012) and Towner *et al*. (2013) have provided estimates for discrete aggregation sites in M.Bay and G.Bay in the Southern and Western Cape Provinces respectively. Towner *et al*. (2013) used dorsal fin images collected over a four year period in G.Bay (January 2007–December 2011) with Schwarz and Arnason's (1996) POPAN version of the Jolly-Seber (JS) model to estimate superpopulation size at 908 individuals (95% CI, 808–1008), but did not present capture, apparent survival or

entry probability estimates. Despite the estimate being relatively high and similar to that of Cliff *et al*. (1996b), this again cannot be considered a national estimate, given that their study was restricted to just one of several major aggregation sites in South Africa. Thus, a national population size estimate is still lacking for the South African stock.

Two studies have presented population size estimates for white shark populations in the Northeast Pacific (NEP) off the Central Californian coast (C.Calif), USA (Chapple *et al*., 2011), and at Guadeloupe Island (G.Island), Mexico (Sosa-Nishizaki *et al*., 2012). Chapple *et al*. (2011) used a „closed" Bayesian model with dorsal fin photo-identification (Photo-ID) data to estimate the subadult and adult white shark population size at 219 individuals (95% CI, 130–275). At G.Island, Sosa-Nishizaki *et al*. (2012) used body pigment patterns from underwater photo-ID records, with the „open" population Cormack-Jolly-Seber (CJS) model (Cormack, 1964; Jolly, 1965; Seber, 1970) and POPAN model to estimate superpopulation size at 120 subadult and adult individuals and high estimates of apparent survival (ϕ = 0.93 ± 0.01 SE). At D.Reef, South Australia, Strong *et al*. (1996) used conventional tag returns and ultrasonic telemetry methods with a basic JS model (Jolly, 1965; Seber, 1965) to estimate white shark population size at 191.7 (95% CI, 36.5–1612.2) and 18 individuals (95% CI, 3.9–157.6) in their second and third expeditions respectively, and particularly low estimates of apparent survival (ϕ = 0.2). Thus, where abundance has been estimated white sharks are considered rare, adding to their vulnerability and warranting concerns over their conservation, globally.

Gaps in knowledge

Cliff *et al*. (1996b) motivated their study by the urgent need to assess the status of the white shark stock in South Africa. Despite their motivation, nearly two decades later the same need for demographic data exists for white sharks throughout much of their range. Knowledge is currently lacking for fundamental aspects of white shark biology, behaviour, demography, and life history. Population sizes and age/sex compositions, as well as growth rates of populations and rates of mortality, survival and emigration all remain poorly understood, and highlight clear gaps in current knowledge. In South Africa, although white sharks are known to undertake coastal and oceanic return migrations (Bonfil *et al.*, 2005), the factors responsible for driving the timing and frequency of movements, dispersal rates and transience, whether ontogenetic, periodic or irregular, and the degree of exchange between aggregation sites or residency times and fidelity within sites, are not well understood. Critical

reproductive sites have not been identified satisfactorily on a global scale. Therefore, migratory pathways between such sites also remain unknown i.e. from nursery areas to pupping grounds and from feeding to mating areas (Cailliet, 1996). Both mating and parturition have yet to be scientifically documented and the reproductive biology, behaviour and physiology of white sharks remain difficult to assess.

Furthermore, the KZNSB nets provide the only long term index of changes in white shark stock structure in South Africa. It is, therefore, crucial that nonlethal monitoring techniques be developed to manage populations of living white sharks elsewhere in South Africa. False Bay"s Seal Island hosts some of the largest white sharks in South Africa and hence presumably a large proportion of the reproductive stock in the region. However, there is reason to doubt the existence of a breeding adult population in False Bay (Kock and Johnson, 2006) and no baseline demographic data exist for this important aggregation site. This clearly demonstrates the direct requirement for this research to assist in overcoming the knowledge deficit.

Dissertation outline, aims and objectives

The aim of this dissertation is to generate base-line demographic data for the aggregation of white sharks at Seal Island, information that might be used to facilitate the development of a management strategy and ultimately assist in their conservation in South Africa. Chapter 1 provides an introduction to the white shark and demonstrates the requirement for this research. Chapter 2 introduces the study area and provides an overview of field research methodology. Chapter 3 presents the first key objective, which developed a dorsal fin image cataloguing system and photo-ID protocol to identify individual white sharks using dorsal fin natural marks. Chapter 4 presents data for inter-annual and inter-monthly trends in effort hours, shark sightings, sighting rate analyses (SPUE) and sex ratios data for the period 2004–2012. The second major objective is therefore to assess both long-term and intra-seasonal dynamics of the aggregation and its sex composition. The third objective assesses frequencies of captures and recaptures from dorsal fin images collected over the same nine-year period. These are used to identify residents and transients, and further to assess site fidelity of both sexes of sharks to Seal Island and whether sharks temporarily and/or permanently emigrate from the population. Annual comparisons are made for numbers of sharks identified (captures + recaptures) with numbers of sharks sighted but photographically unidentified to assess photo-ID efficiency. The final objective in Chapter 4 presents data for the size distribution and maturity composition of

the identified population. Chapter 5 presents the final important objectives of the study, which generated baseline mark-recapture estimates for population size (N), and probabilities of, capture (p), apparent survival (ϕ) and entry of sharks into the population (β),using open(CJS and POPAN) population models. Chapter 6 concludes with a synthesis of the findings of this study and proposes a new life history hypothesis and dispersal mechanism for maturing *C. carcharias* in South Africa.

CHAPTER 2

STUDY AREA AND GENERAL METHODS

STUDY AREA

This study took place at Seal Island (35° 8‟6”S, 18° 35‟00”E) in the north-western corner of False Bay (Figure 2.1) in the Western Cape, South Africa.

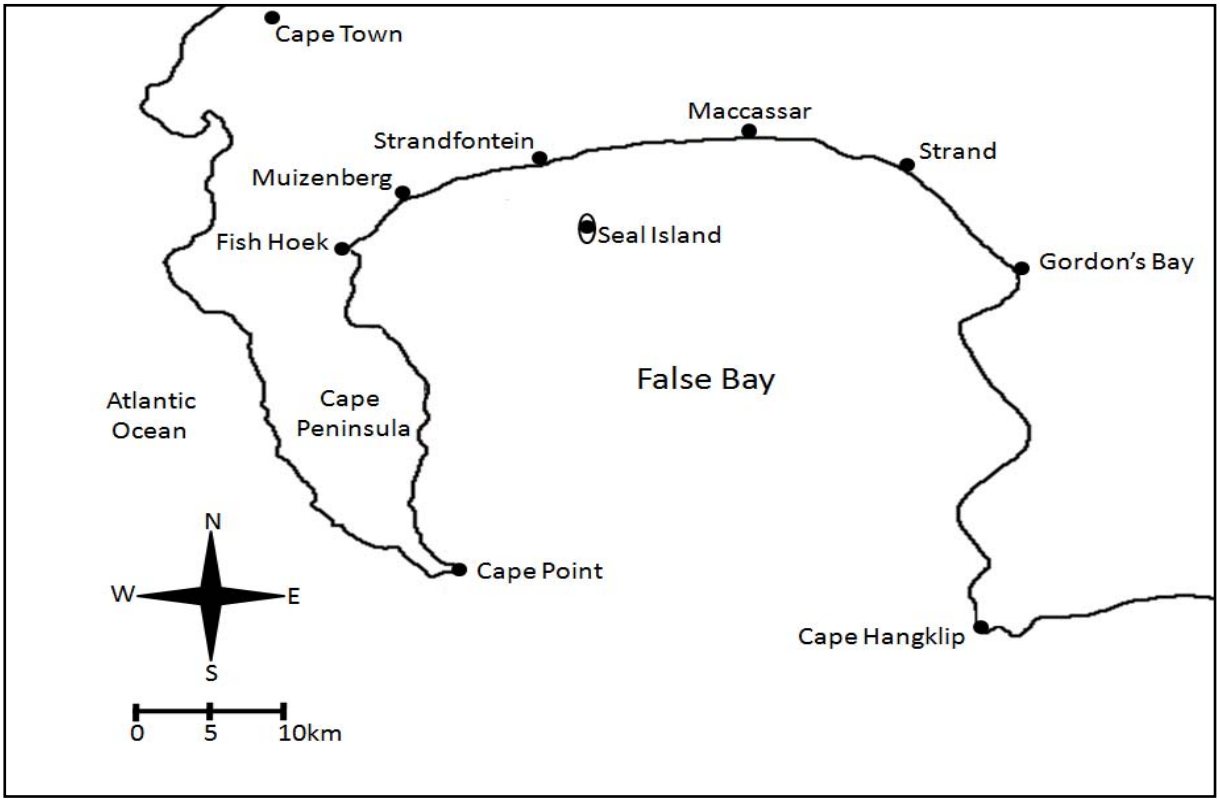

Figure 2.1.Map of False Bay showing Seal Island and other landmarks.

Oceanography and climate

The Southwest Cape climate is distinctly Mediterranean, and thus receives the majority of its rainfall in the winter months of June–August (Spargo, 1991). Sea surface temperature (SST) in winter is approximately 15°C, whereas in summer SST is generally warmer around 19°C. However, in summer months, upwelling results in a seasonal thermocline, which starts in December and is maintained until March, which stratifies and reduces bottom temperatures in the Bay to 1–3°C below average winter temperatures (Grundlingh and Largier, 1991). Water circulation is cyclonic, entering the Bay at Cape Point it is moved by currents along the

western, northern, and eastern margins, and finally exits the Bay around Cape Hangklip. In summer, water circulation slows and the interior of the Bay may become relatively stagnant (Grundlingh and Largier, 1991), which leads to deposition of fine sediments.

Tidal range is modest, with mean high and low water spring tides reported at +0.90 m and −0.58 m, respectively, and the highest and lowest astronomical tides reported at +1.34 m and −0.83 m, respectively, with the tidal gauge set to +0.16 m (Spargo, 1991). Swell origin is predominantly south-west and swell conditions are variable from flat calm (0 m) to large (> 6 m) seas in stormy weather (Pers. obs.). Wind conditions vary from light to gale force. Light northwest winds are predominant in the autumn and winter and strong south-east winds in the spring and summer (Grundlingh and Largier, 1991).

Seal Island

Seal Island is a small (400 × 50 m), low lying (< 10 m above sea level) elongated outcrop of Malmesbury shale, and the only true island in False Bay (Spargo, 1991) of approximately 6 ha in area, with its long axis is oriented north-south. The northern and eastern waters surrounding the island are shallower than the southern and western quadrants, which are starkly different and characterised by deep-water drop-offs. Submarine habitat at the northern end is characterised by a large granite plateau comprising large flat boulders (Du Plessis and Glass, 1991), for which the depth profile steadily decreases heading north away from the island, giving way to a predominant sand bottom, punctuated by reef, at a maximum depth of approximately 25 m (Unpublished side-scan sonar data 2012). On the eastern side a shallow channel runs parallel to the island and separates two submerged outer-lying reefs.

Seal Island is a Provincial nature reserve (Spargo, 1991), which supports various marine birds, such as *Spheniscus demersus*, *Larus dominicanus*, *Phalacrocorax capensis* and *Morus capensis*. Seal Island currently forms a permanent haul out site and important breeding colony for the Cape fur seal (*Arctocephalus pusillus*), for which annual abundance estimates range between 36,000–77,000 individuals (Kirkman *et al*., 2006) and fluctuate most dramatically in the breeding season (November–February). Post-partum, juvenile seals are rapidly nursed (February–March) and introduced to the ocean, where pups must first learn how to swim before foraging can commence out in the Bay and eventually further out at sea. The primary seal departure and arrival point is located off the southern terminus of the island, a small craggy outcrop and shallow reef area known locally as “the launch pad”, where seals congregate in small groups, before launching from this area (Laroche *et al*., 2008).

White sharks are present in False Bay throughout the year, but utilise at least two distinct regions within the Bay. Females predominate inshore in spring–summer, whereas both sexes occur in approximately equal proportions at Seal Island in autumn–winter. Large white sharks are regularly observed preying on juvenile fur seals (~4–8 months old; Figure 2.2) within this period (Kock, 2002; Hammerschlag *et al*., 2006; Laroche *et al*., 2008),when inexperienced, predator-naïve seal pups, that are presumed to be easily captured prey compared to adult conspecifics, are most available to them (DeVos, 2010; Kock *et al*., 2013). Blubber rich seals present a significant nutritional source for large white sharks and are thus presumably desirable prey items to fuel their high metabolic demands (Estrada *et al*., 2006; Semmens *et al*., 2013). Consequently, the white shark aggregation at Seal Island is thought to form in response to seasonal abundance and accessibility of fur seal prey (Kock and Johnson, 2006; Kock *et al*., 2013). The result is that Seal Island forms one of the most important areas known globally for pinniped hunting white sharks.

Figure 2.2.White shark hunting a juvenile Cape fur seal at the south-western end of Seal Island.

SURVEY METHODS

Overview

Over a nine-year period (2004–2012), routine baited surveys were conducted in autumn, winter and early spring months (range February–October) around Seal Island. Observations were made and photographs were taken from the research vessel "*Xiphodon*", an 8.0 m long power-driven catamaran with 2 ×115 hp petrol engines. The vessel was anchored in position for each survey, once a suitable location had been determined (Figure 2.3); a decision primarily dictated by sea and wind conditions and prior knowledge of shark activity.

Anchorage at the southern end of Seal Island was preferred when conditions allowed, however, sampling also took place off the northern end on occasion, generally during February and March during exploratory trips early within a season. Total baiting time was recorded for each sampling occasion and was used to assess trends in effort and shark sightings rates (see Chapter 4). Given the small area of Seal Island, short distances between anchor sites (± 500 m), and the propensity for white sharks to move and hunt all around the island, observations from different anchorage sites were not considered independently. Thus, the size of the study site was constant as Seal Island (see Chapter 5).

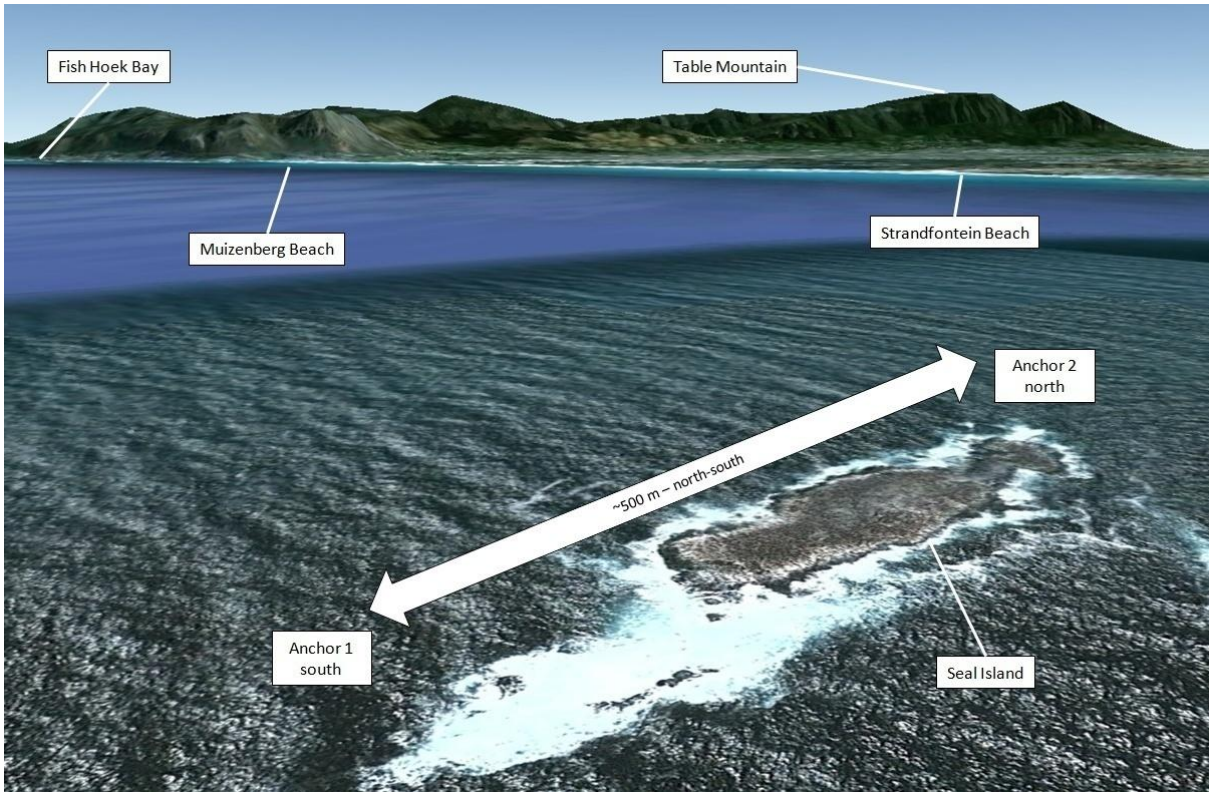

Figure 2.3.Image of Seal Island showing surveyed sites and their approximate distance apart.

Shark attraction and manipulation

Aggregation sites, like the seal colony in False Bay, provide excellent opportunities to study white shark population biology (Ferreira and Ferreira, 1996; Strong *et al*., 1992, 1996; Domeier and Nasby-Lucas, 2007; Chapple *et al*., 2011; Sosa-Nishizaki *et al*., 2012; Nasby-Lucas and Domeier, 2012; Towner *et al*., 2013). Although naturally present at these sites, white sharks are elusive, notoriously difficult to study and can rarely be sampled randomly (Cailliet, 1996). To increase sighting rates sharks are typically attracted to an observation site using visual cues or olfactory attractants (Nelson and Gruber, 1963; Kelly and Klimley, 2003; Meekan *et al*., 2006). White sharks, similar to other large sharks, are most reliably attracted using baits and olfactory stimuli, thus baiting techniques are widely applied in large shark field research (Klimley and Anderson, 1996; Strong *et al*., 1996; Heithaus *et al*., 2002; Domeier and Nasby-Lucas, 2007; Sosa-Nishizaki *et al*., 2012).

White sharks were attracted in this study using minced oily fish products, such as mashed sardine (*Sardinops sagax*), which was typically combined with shredded fish, such as snoek (*Thyrsites atun*), or tuna, like skipjack (*Katsuwonus pelamis*), yellowfin (*Thunnus albacores*) or longfin (*Thunnus alalunga*). Small chunks of marine mammal blubber and oil (*Eubalaena australis*) were used in 2004–2006. Fresh sea-water was added to the mashed bait, mixed, and then dispersed overboard at regular intervals over the duration of each survey (never exceeding 1 L min^{-1}).

A small piece of bait, such as a tuna head, was attached to a rope with a float and was used as a visual stimulus to lure and manipulate sharks into exposing their dorsal fins within photographic range of the vessel (5–10 m). Although baiting created a non-natural scenario, it provided the opportunity to interact with sharks regularly and reliably, which increased the likelihood of visible contact time (Bruce and Bradford, 2011), assisted with routine sighting surveys (i.e. minimum counts of different sharks present during each survey) and facilitated dorsal fin mark-recapture studies using surface based photo-identification (photo-ID) techniques. Effects of provisioning have been demonstrated to be minimal on white shark behaviour at this aggregation site (Laroche *et al*., 2007).

CHAPTER 3

USING DORSAL FIN NATURAL MARKS TO IDENTIFY WHITE SHARKS

INTRODUCTION

Estimation of abundance and other demographic parameters for wildlife populations can be accomplished using one of four data-types: age-ratios, dead-recoveries, radio-telemetry, or live-encounters (Sandercock, 2006). Age-ratio studies are not practical for monitoring white shark populations, as no method is currently available to age this species in field studies. White sharks also suffer low natural mortality and this, combined with poor capture rate reporting from fisheries, which generally go underreported for fear of reprisals due to protective legislation (Cliff *et al*., 1996b), negate the use of dead-recovery methods. Radio-telemetry is a key monitoring tool for wildlife species and is especially important for survival analyses based on a range of different statistical procedures (Williams *et al*., 2002). However, behavioural telemetry studies utilize expensive technology, making costs of transmitters prohibitive and tracking effort restrictive in terms of the number of individuals that can be monitored in a population (Sandercock, 2006). Live-encounter mark-recapture studies therefore remain the only feasible method available for long-term demographic research on many wildlife populations (Sandercock, 2006), particularly for vulnerable species (Willson *et al*., 2011), for which lethal sampling is inappropriate.

With the advent of suitable tracking technology, a number of studies have demonstrated that white sharks commonly venture thousands of kilometres into the open ocean where they can spend months at a time, and regularly undertake long distance coastal migrations (Boustany *et al*., 2002; Bonfil *et al*., 2005; Bruce *et al*., 2006; Weng *et al*., 2007a, 2007b; Domeier and Nasby-Lucas, 2008, 2012; Nasby-Lucas *et al*., 2009; Bonfil *et al*., 2010; Jorgensen *et al*., 2010, 2012). However, white sharks also demonstrate strong seasonal trends in fidelity to specific sites, which provide excellent opportunities to gather demographic data and promotes the use of mark-recapture methods for long-term monitoring research (Bonfil *et al*., 2005; Bruce *et al*., 2006, Domeier and Nasby-Lucas 2007, 2008; Jorgensen *et al*., 2010; Nasby-Lucas and Domeier, 2012).

Mark-recapture data for white sharks can be acquired from direct observation (Cailliet,1996), conventional tagging studies (Cliff *et al*., 1996b; Ferreira and Ferreira, 1996;

Strong *et al*., 1996), radio telemetry (Strong *et al*., 1996), and photo-identification (photo-ID) of natural markings (Anderson and Goldman, 1996; Anderson *et al*., 1996, 2011; Domeier and Nasby-Lucas, 2007; Chapple *et al*., 2011; Nasby-Lucas and Domeier, 2012; Sosa-Nishizaki *et al*., 2012; Towner *et al*., 2013). Mark-recapture methods have been used to study white shark population dynamics (Ferreira and Ferreira, 1996) and sex differences within aggregations (Nasby-Lucas and Domeier, 2012), but most notably to yield estimates of population size (Cliff *et al*., 1996b; Strong *et al*., 1996; Chapple *et al*., 2011; Sosa-Nishizaki *et al*., 2012; Towner *et al*., 2013), apparent survival (Strong *et al*., 1996; Sosa-Nishizaki *et al*., 2012) and mortality (Cliff *et al*., 1996b).

Conventional tagging studies can be applied in the context of dead-recapture or live-encounter, and have received considerable attention from wildlife biologists and statisticians interested in developing applied statistical models to estimate animal abundance (Pollock *et al*., 1990). However, while these studies can provide a means to census a population, they are expensive and take considerable effort over many years (Chapple *et al*., 2011), and are difficult to perform due to the large size and intractability of some shark species (Kohler and Turner, 2001). In addition, under reported tag recaptures (Cliff *et al*., 1996b), tag bio-fouling, tag shedding and misidentification (Kohler and Turner, 2001; Dicken *et al*., 2006), often preclude their long-term use, particularly for white sharks (Anderson *et al*., 2011).

Photo-ID is an alternative live-encounter mark-recapture method, used to monitor wildlife species that bear distinctive features, specifically natural markings such as pigmentation patterns, scars and amputations, or notches in anatomical features, such as dorsal fins. Photo-ID is non-invasive and relatively cheap to administer and provides a particularly powerful and efficient tool. Individuals can be photographed consistently over long periods of time, given there is no direct effect on study subjects as no physical capture takes place i.e. animals are "captured" only in an image. Therefore, photo-ID is conservation consistent in its approach, which is an essential attribute for research on vulnerable species.

The photo-ID technique was pioneered in the mid 1970"s on cetaceans and received widespread use thereafter on marine mammals (Würsig and Jefferson, 1990; Karczmarski and Cockcroft, 1998; Wilson *et al*., 1999; Calambokidis *et al*., 2004; Mizroch *et al*., 2004; Coakes *et al.,* 2005). More recently, photo-ID has been used to study populations of various other aquatic and terrestrial species, including pinnipeds (Vincent *et al*., 2005), manatees (Langtimm *et al.,* 2004), otters (Gilkinson *et al.,* 2007), cheetahs (Kelly, 2001) and salamanders (Gamble *et al.,* 2008). Although photo-ID studies of elasmobranchs are

relatively recent, the technique has been used to successfully identify individuals within populations of various shark and ray species (see Marshall and Pierce, 2012 for a review).

Photo-ID studies on sharks and rays have primarily used natural pigment patterns, dorsal fin shape, or scar markings to assist with identification (Anderson and Goldman, 1996; Anderson *et al*., 1996; Klimley and Anderson, 1996; Sims *et al*., 2000; Castro and Rosa, 2005; Porcher, 2005; Domeier and Nasby-Lucas, 2007; Graham and Roberts, 2007; Speed *et al*., 2007; Dudgeon *et al*., 2008; Buray *et al*., 2009; Gubili *et al*., 2009; Holmberg *et al*., 2009; Rowat *et al*., 2009; Riley *et al*., 2010; Anderson *et al*., 2011; Brooks *et al*., 2011; Chapple *et al*., 2011; Jewell *et al*., 2011; Marshall *et al*., 2011; Nasby-Lucas and Domeier, 2012; Sosa-Nishizaki *et al*., 2012; Towner *et al*., 2013).

Photo-ID studies have been used to estimate elasmobranch growth rates (Sims *et al*., 2000; Graham and Roberts, 2007) and longevity (Anderson *et al*. 2011), assisted in defining reproductive cycles (Porcher, 2005; Nasby-Lucas and Domeier, 2012) and sex differences within aggregations (Marshall *et al*., 2011; Sosa-Nishizaki *et al*., 2012), and have also been used to identify trends in site fidelity (Domeier and Nasby-Lucas, 2007, 2012; Anderson *et al*., 2011; Chapple *et al*., 2011; Marshall *et al*., 2011; Nasby-Lucas and Domeier, 2012), generate estimates of population size and structure (Castro and Rosa, 2005; Meekan *et al*., 2006; Holmberg *et al*., 2009; Rowat *et al*., 2009; Chapple *et al*., 2011; Marshall *et al*., 2011; Sosa-Nishizaki *et al*., 2012; Towner *et al*., 2013) and to monitor tag retention-times (Dudgeon *et al*., 2008; Jewell *et al*., 2011).

Nasby-Lucas and Domeier (2012) used underwater images of body pigment patterns to identify 113 subadult and adult white sharks at Guadeloupe Island over a nine-year period. Sosa-Nishizaki *et al*. (2012) analysed this data set using the POPAN model to estimate superpopulation size at 120 individuals. Chapple *et al*. (2011) used dorsal fins and natural marks to estimate the subadult and adult white shark population size off Central California at 219 individuals. The most recent photo-ID study on white sharks used dorsal fin images collected over a four-year period in Gansbaai, South Africa, to estimate superpopulation size for this aggregation site at 908 individuals (Towner *et al*., 2013).

Thus, photo-ID studies are a viable and reliable means for estimating white shark population size. Furthermore, Bonfil *et al*. (2005) used pop-up archival satellite tags (PAT), combined with photo-ID, to document the transoceanic-return-migration of a 380 cm TL (total length) female white shark from South Africa to Australia. This adolescent shark was identified upon her return to South Africa from a dorsal fin image, demonstrating the long-term value of photo-ID, particularly once tag-battery lives are exhausted and/or tags are shed.

MATERIALS AND METHODS

Field-identification protocol

During each survey at least one (usually two) experienced field biologists were present at all times, often with the addition of trained research interns, who assisted with observations and recording of information. All crew members searched for sharks with the naked eye from the lower and upper decks of the vessel for the full duration of each survey period. During routine (i.e. sightings) and photo-ID surveys, the total number of different sharks sighted was recorded. Individual sharks were distinguished between based on sex (presence or absence of claspers), behaviour, body colour and size (estimated to the nearest 0.5 m with reference to the vessel stern width of 2.6m), and from dorsal fin shape, size and the presence or absence of pigmentation spots (black) or blemishes (white) on the fin.

Other features used included natural body markings (e.g. pigments on the gills, caudal and pelvic fins) and non-natural marks (e.g. bite marks, fresh wounds (red, pink, and white) and healed scars (black), tags (conventional and telemetry), fishing equipment (hooks, line, traces, lures and floats), fin amputations and structural damage). Body deformities (e.g. scoliosis), dense parasite colonies, or any other visible characteristics were also utilised for short-term identification of sharks within a season. Unless the feature was distinct and obvious, or considered as a mark that would persist long term (e.g. a missing pectoral fin), rarely was any one characteristic used to identify individuals to avoid duplicating counts. The nature of the body marks largely dictates the duration over which they may, or perhaps more importantly, should be used, to reliably identify among white sharks in long-term studies. Although every effort was made to reduce misidentification, some bias is likely to have occurred from sighting surveys. Regardless, sightings records do provide a basic, but valuable representation of population composition, although actual abundance is overinflated from sightings.

Photographic-identification protocol

Dorsal fins were photographed during each photo-ID survey. At all times an experienced photographer was responsible for capturing dorsal fin images. Each time a fin broke the surface a sequence of 2–10 images were taken for each pass of a shark, using a Canon 40D digital SLR camera (10.1 megapixels), fitted with a 70–300mm f/4-5.6 Canon EF lens. Taking a sequence of images using the motor drive facility of the camera maximised the

probability of capturing “good” quality, high resolution images, which were in focus, displayed as much of the fin as possible at a preferred angle at 90°perpendicular, and had variable contrasting backgrounds to the image. In a scenario where „well known“ individuals were reencountered over subsequent capture occasions, photographs were still taken until „good“ quality images were obtained for both sides of the fin during every survey. Inevitably, every dorsal fin was not captured on each occasion (see Chapter 4), due to the behaviour of individual sharks and photographer response times.

Organising images

To avoid confusion during the image sorting process, image capture times on all cameras and the stop-watch used during observations were calibrated to the exact same time. Therefore, all images could be reliably matched to field observations in a systematic manner. Images were downloaded daily and imported into folders arranged in a hierarchical format (year > month > date), with each „date“ folder representing each photo-ID survey or capture occasion. Within each date folder images were organised into a unique coded reference folder for each individual. As an example, the folder structure for the seventh shark captured on 1June 2012 was:

2012 > June > 010612 > 007-010612

Overview: Image cataloguing

Surveys took large numbers of photographs, of which only a small number of good quality images were retained. Poor quality, blurred images were immediately deleted when identifiable marks could not be discerned confidently. Initially, automated recognition software, specifically the program DARWIN-FINSCAN (Stanley, 1995), was assessed to develop the photo-catalogue. Unfortunately, data loss was unacceptable using this approach, which was thus abandoned, and the decision was made to match images visually.

A folder (interim-catalogue) was created to contain all of the unique individuals as they were identified as new sharks (i.e. captures), starting with the first image taken in June 2004 (WS0001). All subsequent images (in chronological order) were compared to the interim-catalogue to identify new captures, or recaptures of known sharks. Recapture records were inputted into an Excel spreadsheet to develop (interim) capture histories for all sharks (n = 372). However, at this stage images were matched without the assistance of any specific computer-assisted software, which lacked searchable criteria, and hence lacked the ability to

search among fins for natural mark features. Given that each new image had to be cross-referenced against 372 individuals (500+ images), the interim-catalogue was laborious and time consuming to implement.

Consequently, image-cataloguing software, Adobe Lightroom III, was used. This offered major benefits, such a built-in search facility based on keywords (Ryklief, 2012), manipulating images *in-situ* as required (e.g. exposure, cropping) and grading (see "image grading" below) to assess their quality using a similar protocol to Anderson *et al*. (2011) and Chapple *et al*.(2011). Re-cataloguing each image into Lightroom (repeating the above process) provided the opportunity to search for false positives and to detect any misidentification errors in the *interim*-catalogue, which were found to be negligible.

Lightroom: Image quality and editing

Only "good" quality images (i.e. dorsal fin was close to perpendicular to the camera (45–90°), entirely in the frame, clearly focussed and otherwise of sufficient quality such that subtle markings could be reliably identified, were retained in the unique coded reference folder for each individual in each capture occasion, within the photo-database. All good quality images were retained in the database in case additional images were required to cross reference a specific fin feature in the catalogue, once potential but ambiguous matches were found. Images were edited to improve composition and exposure, and were cropped to standardise fin size and trailing edge orientation, which facilitated the matching process.

Image grading

The „best" left and/or right hand side image(s) for each shark was selected for grading from the unique coded reference folder(s), and assigned points using the following criteria: (i) *angle* of dorsal fin trailing edge (TED): (a) < 45 °, and (b) ~45–90° angle(s), scored 1 and 2 points, respectively, (ii) *exposed* proportion of the dorsal fin TED above water: (a) < 50%, (b) ~50–75%, and (c) >75%, scored 0,1, and 2 points, respectively, (iii) image *focus* and *clarity*: (a) *slight* pixilation, (b) *no* pixilation, scored 1 and 2 points, respectively, and (iv) image *contrast*: (a) portions of fin TED not distinct from background, or (b) >75% of TED distinct from background, scored 1 and 2 points, respectively.

Points were tallied for each graded image and a keyword reference number (see "keywords and image search criteria" below) ranging between 1 and 8 was assigned to each image in the database. Images graded <6 points were assigned the appropriate keyword

number (1–6) and were excluded from further analysis, with a few exceptions. Single images graded < 6 points that could not be unambiguously matched were always excluded. However, in instances where an image had been graded < 6 points and a recapture was confirmed from that image, for a particularly well-known individual, the image was retained and was used to contribute to an individual‟s encounter history, provided at least three mark types were identical in the catalogue reference image. Although single images graded < 6 points were excluded from this study, and few matches were typically found for these sharks, the images may still be of some future utility, as images are acquired that can be matched.

All images graded > 7 points were assigned keywords (7 or 8) and retained in the database for subsequent matching to reference images in the catalogue. All graded images were independently assessed by A. Kock as a further check to account for observer bias, with any images considered ambiguous at this stage excluded from further analysis, regardless of the point grading system. Thus, confidence is high that misidentification error was low and any resulting bias introduced was negligible.

Keywords and image search criteria

To assist with the visual matching procedure, a filter system based on searchable „keyword‟ criteria was developed using the built-in utility in Lightroom (Ryklief, 2012), which reduced the potential number of candidates by searching for dorsal fin images with shared physical characteristics or natural marks (summarised in Table 3.1). Keywords were assigned to each graded left- and right-hand-side image in the database, based on the profile/shape of the fin tip, which enabled a quick search for obvious tip features, such as amputated, pointed, rounded, squared-off, and other (Figure 3.1.A, B, C, D, and E, respectively). To further refine searches, keywords were assigned based on the dorsal fin trailing-edge structure, which ranged from featureless to gouged and notched (indentations), and spiked and lobed (protrusions), and combinations thereof (Figure 3.2.A, B, C, D, and E, respectively). Indentations were features that indented obviously past the general mid-line of the trailing edge, while a protrusion was a feature that protruded obviously out past the mid-line.

In addition, keywords were assigned for dorsal fin pigments, both white blemishes (Figure 3.3) and black spots (Figure 3.4). As an example, white pigment present on the left-hand-side of the fin was coded as WP-L*p,* white pigment absent was coded as WP-L*a*, and when pigments, in this case white, could not be discerned reliably (due to relatively poor quality, obscure angles, or obstruction by water), the image was coded as WP-L-*n/o*.

Italicized lower case letters (*p, a* and *n/o*) indicate that pigments were either *present, absent,* or *not-obvious*, respectively. The process was repeated assigning the appropriate keywords for white pigments for all right-hand-side images. Similarly, equivalent keywords for black pigments were assigned to all images. If pigments were suspected to be present, from field-based observations, or the image itself, the appropriate keyword was assigned in addition to *not-observable*, to increase flexibility in the search process. When metadata were available, keywords were also assigned to images for sex, size i.e. total length (TL) and maturity status (based on TL), with TL estimates defined into 49 cm categories to assist in summarising the data appropriately, and reducing potential bias from observer error. The final keywords applied to images were the unique catalogue ID reference codes (WSxxxx).

Table 3.1.List of keywords used to catalogue *Carcharodon carcharias* dorsal fins.

Feature			Keyword	Description	Image ref.
Image side:			Left		
			Right		
Sex:			Male		
			Female		
			Unsexed		
Size (cm):			150-199		
			200-249		
			250-299		
			300-349		
			350-399		
			400-449		
			450-499		
			500-549		
			550-599		
			600+		
			Unknown size		
Maturity:		Male:	Immature (149-299 cm)		
			Subadult (300-349 cm)		
			Mature (> 350 cm)		
		Female:	Immature (< 399 cm)		
			Subadult (400-449 cm)		
			Mature (> 450 cm)		
Dorsal fin:	Tip:	Shape:	Amputated	Fin tip completely missing	Fig.3.1.A
			Pointed	Specific 'pointed' tip to apex of fin	Fig.3.1.B
			Rounded	No specific fin tip, curved over apex of fin	Fig.3.1.C
			Squared-off	Squared off overhang from tip apex	Fig.3.1.D
			Other	Tip shape not easily/obviously interpreted	Fig.3.1.E
	Trailing edge:	Structure:	Featureless/flat	Relatively uniform, flat, and featureless	Fig.3.2.A
			Gouged	'U' shaped indentation (symmetric/asymmetric)	Fig.3.2.B
			Notched or double-notched	'V', or 'W' or 'V¯¯¯V' shaped indentation	Fig.3.2.C
			Spiked	'V' shaped protrusion	Fig.3.2.D
			Lobed	'U' shaped protrusion	Fig.3.2.E
	Pigment:	White:	WP-L*p*	White pigment *present* left hand side	Fig.3.3
			WP-L*a*	White pigment *absent* left hand side	
			WP-L-*n/o*	White pigment *not obvious* left hand side	Fig.3.5
			WP-R*p*	White pigment present right hand side	
			WP-R*a*	White pigment absent right hand side	
			WP-R-*n/o*	White pigment not obvious right hand side	
		Black:	BP-L*p*	Black pigment present left hand side	Fig.3.4
			BP-L*a*	Black pigment absent left hand side	
			BP-L-*n/o*	Black pigment not obvious left hand side	
			BP-R*p*	Black pigment present right hand side	
			BP-R*a*	Black pigment absent right hand side	
			BP-R-*n/o*	Black pigment not obvious right hand side	
Cat-ID ref.#			WS0001; WS0002...	Unique identification reference code	Fig.3.6

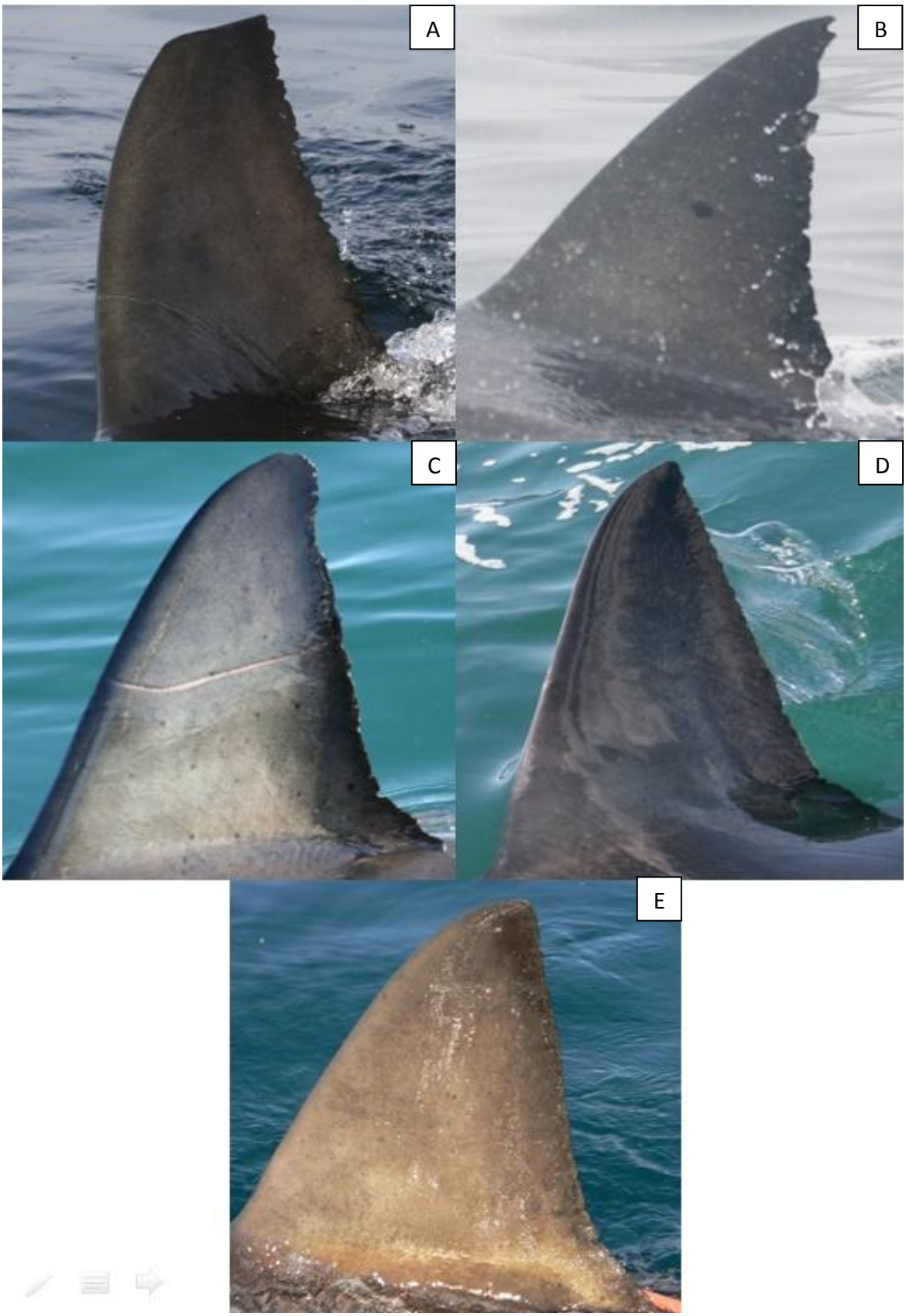

Figure 3.1.Examples of white shark dorsal fin images, which highlight the fin tip features used to identify individuals (A = amputated, B = pointed, C = rounded, D = squared off and E = other).

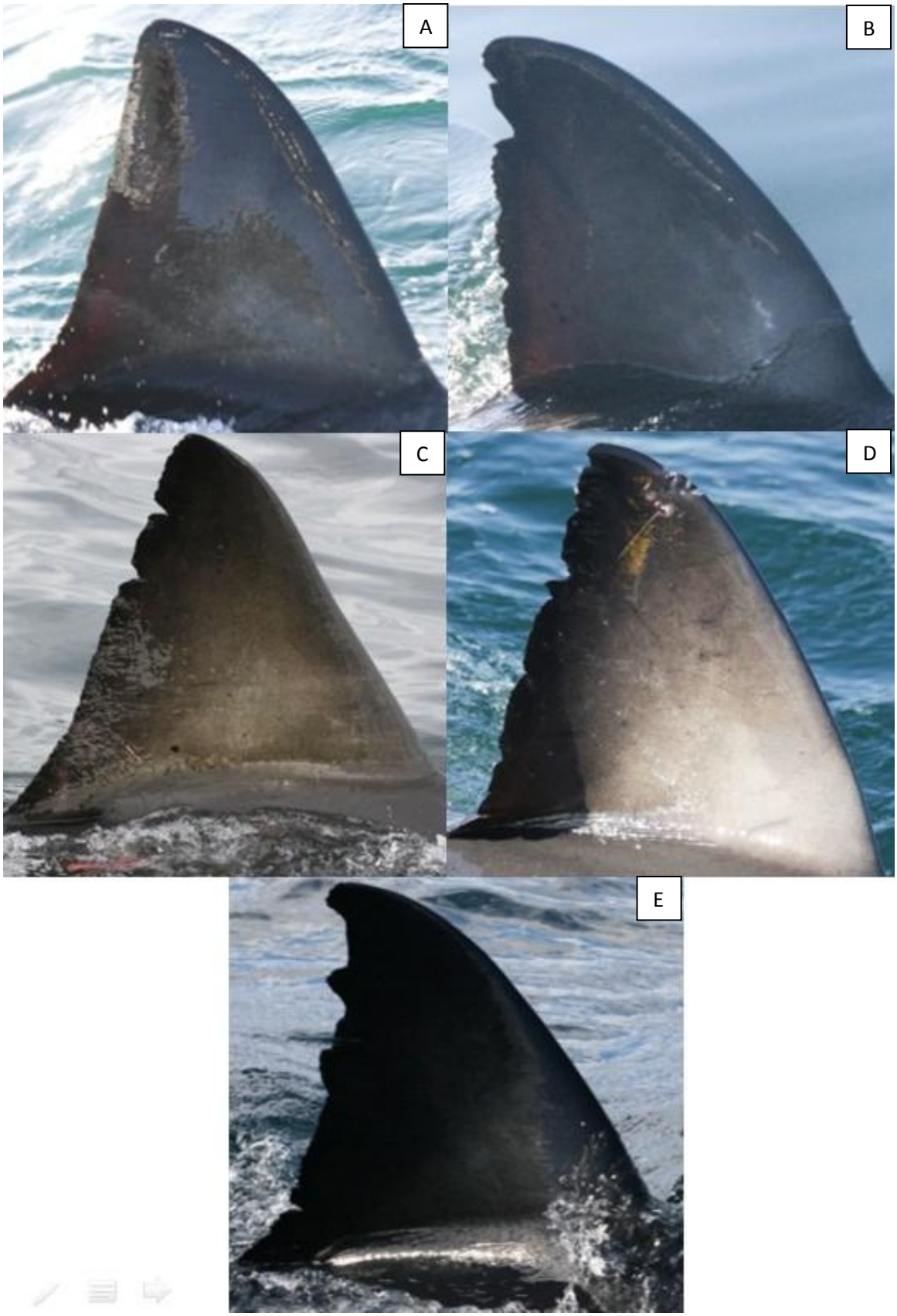

Figure 3.2.White shark dorsal fin images of natural mark types on the trailing edge of the fin used for identification (A = featureless, B = gouged, C = notched, D = spiked, E = lobed).

Figure 3.3.Dorsal fin images showing white pigmentation blemishes.

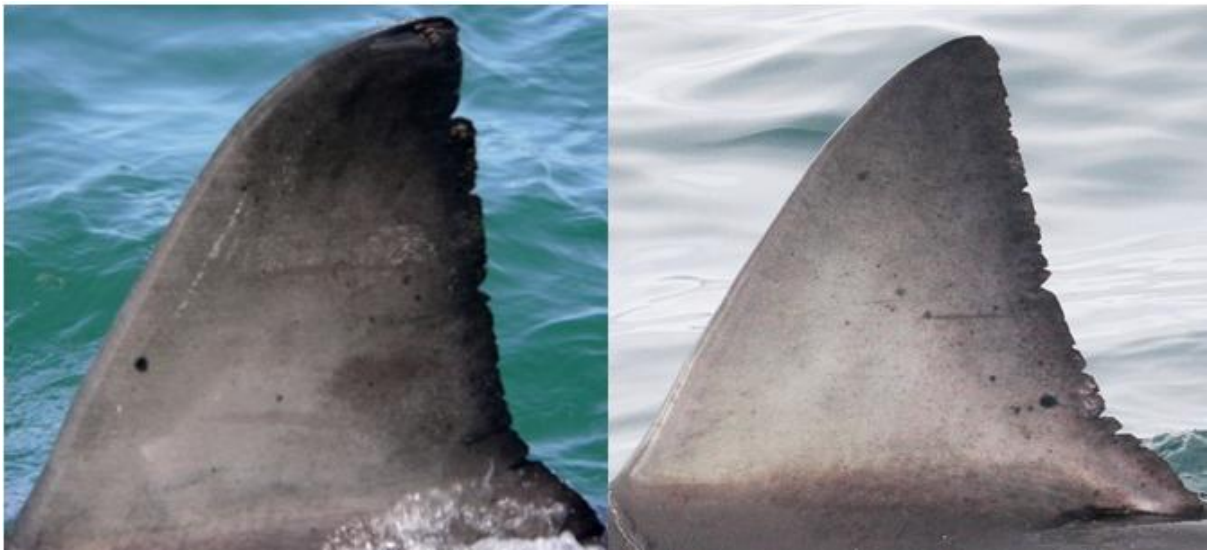

Figure 3.4.Dorsal fin images showing black pigmentation spots.

Image matching

Once keywords were assigned to graded images in the database, the best image for each shark was imported into the catalogue and filtered through the keyword system to search for matches, which were confirmed or rejected visually, based on as many unique identifying marks as possible. Searches based on single identifying marks (e.g. white pigment only) were avoided as standard operating procedure. White pigment blemishes, when they were present, were typically observed close to the base of the leading edge of the dorsal fin. A complication can thus arise when an image shows the fully exposed trailing edge of the fin, but the lower half of the leading edge may be submerged below water. If the pigment mark was faint and

contrasted with white frothy water around the fin, or the lower anterior section of the fin was submerged and/or fully obscured by dark water, it was impossible to determine the presence or absence of white pigment unambiguously (Figure 3.5). Under such a scenario, fin shape, fin-tip profile, and trailing edge structure were still used as reliable identification features.

Figure 3.5.Left and right hand side dorsal fin images for white shark WS0231, clearly showing multiple different natural mark-types used to assist with identifying individuals reliably, when other features may not have been observable.

Furthermore, the same-sided reference image as the candidate image to be matched (i.e. left and left) could not always be searched. At times, candidate images were matched to a single (opposite-sided) counterpart image in the catalogue. As such, having images for both sides of the fin was preferred, but was not essential, provided the lone reference image in the catalogue was high quality, which enabled further comparisons with single candidate image(s) (either side of the fin) confidently, albeit cautiously. A further complication could

arise when a filter was applied using any side-specific characteristic e.g. WP-Lp (white pigment present left-hand-side), as search effort focussed on all left-hand-side images, to the exclusion of right-hand-side images. If the image was not matched the search criteria were broadened and generalised to inspect images of both sides of the fin. This approach was flexible and the combination of search characteristics proved particularly powerful and matched individuals rapidly and reliably. Overall, using keyword filters reduced the amount of time needed to detect recaptures, and whilst filters were very effective at achieving this objective, the system could not be used as a finite method to determine irrevocably whether an individual was a new capture in the study, when no match was found.

Auxiliary identification features

As standard practice natural marks on the fin were used to confirm recaptures of known individuals, or captures of new individuals. However, on rare occasion, *auxiliary* (non-natural) marks on the body or fin, which were present in the same image, were used to confirm the identity of an individual. This was particularly important in the case of WS0226 (Figure 3.6). In 2009, WS0226 was photo-captured and tagged with an acoustic transmitter (at the base of the dorsal fin on the right-hand-side), and was recaptured in 2011. After having sustained severe structural damage to the fin, the trailing edge could no longer be used to identify this individual in subsequent encounters. However, black and white pigments were used in conjunction with the tag stalk (*auxiliary feature*), which remained at the base of the fin once the transmitter had been shed. Major damage to the fin of this nature then in itself became a permanent identifying mark for this particular white shark.

Captures and recaptures

New captures were stringently evaluated before inclusion into the catalogue, and hence the study. Once all relevant keyword searches had been exhausted and if no match was found using this approach, the entire catalogue was searched without filters, cross-referencing the candidate image to all other individuals in the catalogue (both left- and right-hand-side images, similar to the interim-catalogue method). If a match was still not found at this stage the candidate image was considered a new capture or newly-marked shark in the study. New captures were assigned the next available catalogue-ID reference number (CAT-ID Ref # WSxxxx). The process was repeated for every image for which no match was found using filters, before an individual could be irrevocably added as a new capture. Each unambiguous

match of a graded candidate image (7 or 8 points) from the database, with a graded (7 or 8 points) reference image in the catalogue, was considered a recapture of an individual. The candidate image from the database was assigned the same unique catalogue-ID reference number (CAT-ID Ref # WSxxxx) when a match was found. In Figure 3.6, the candidate image on the right (2012) from the database was matched to the catalogue reference image on the left (2005), and the individual was assigned the reference code WS0001.

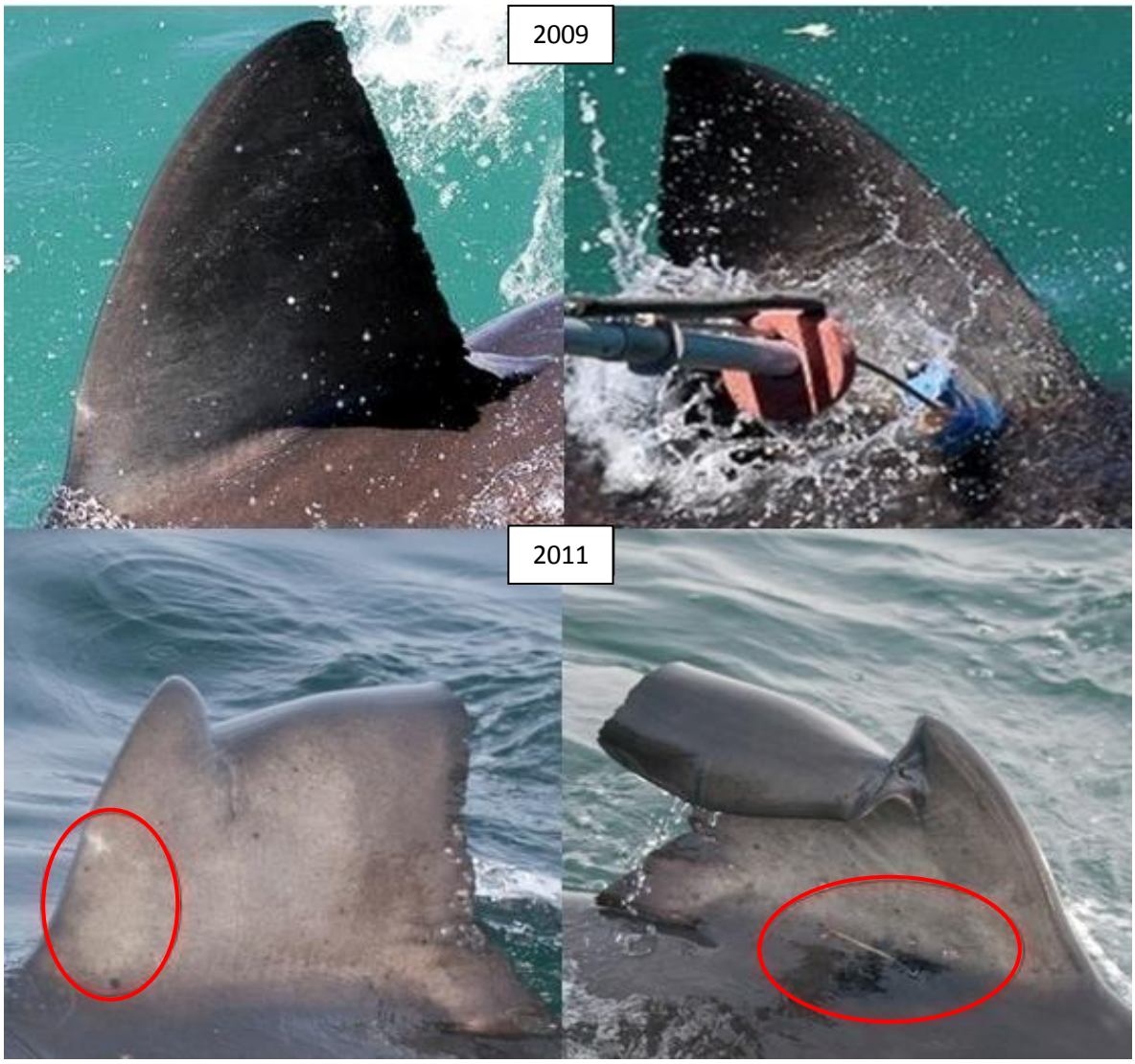

Figure 3.6.Images of structural damage to the dorsal fin of WS0226 taken two years apart (inshore$_{2009}$, Seal Island$_{2011}$) showing *auxiliary* marks used to reliably identify individual white sharks.

Upgrading and adding counterpart images to the catalogue

If the total number of points for the candidate image being matched was equal to or greater than the number of points assigned to the catalogue reference image, and if the candidate image was considered a better representation of dorsal fin features (i.e. identifiable marks

were more visible and/or numerable, a greater proportion of the fin was exposed, with better lighting conditions, contrast and/or angle of the fin), the reference image was replaced. Hence, for recaptures, the catalogue was continually evolving and was regularly refreshed with better quality images, counterpart images, and perhaps more importantly, the catalogue reference images were updated to reflect the current state of the fin to keep track of individuals over long periods of time, in the case of this study nearly a decade.

Figure 3.7.Left-hand-side dorsal fin images for the same white shark (WS0001) showing the unique identification reference code used to identify each individual.

Individual master folder and encounter history information

All matched images (recaptures) to an existing image(s) in the catalogue were exported to a uniquely referenced "master" folder for that particular individual. Master folders were named using the catalogue-ID reference code format (WSxxxx), with sub-folders arranged hierarchically by years and dates of recapture (Figure 3.8). A „master folder" was created for each new capture using the next available reference code assigned from the catalogue. Master folders contained all of the images for each identified individual, and hence contained all of the mark-recapture data required to structure the capture histories. As a final check, all matched images within an individual"s master folder were checked against each other to reduce false positives and potential bias from misidentification. No errors were found at this stage.

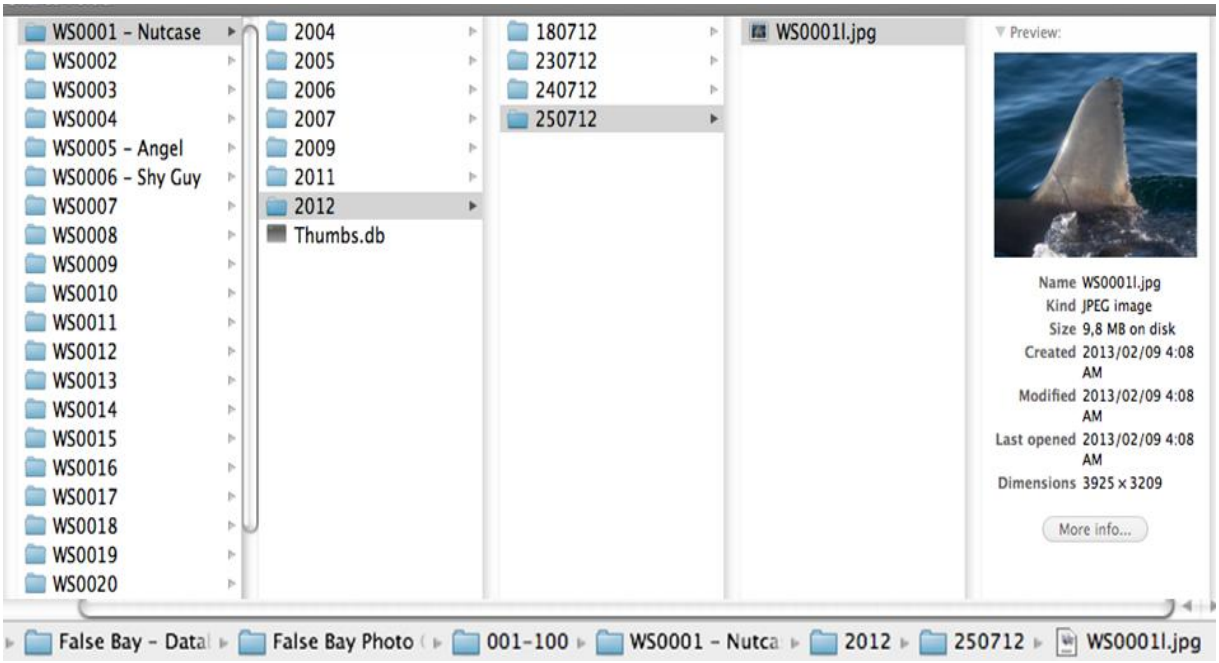

Figure 3.8.Individual master folder setup for WS0001, showing his last recapture dates in 2012.

Capture histories

The first step in a mark-recapture analysis requires that capture histories are created for all of the uniquely marked and identified individuals in the population. Capture histories were compiled in Microsoft Excel and then collapsed into a simple annual indicator of shark absence or presence with nine occasions i.e. years. The encounter history for WS0001 was:

111101011: 1 0 0

This demonstrates capture in 2004, recapture each year until 2007, not present/identified in 2008 or 2010, but recaptured in 2009, 2011 and 2012. The underlined three digit code denotes the „group" to which each shark was assigned based on sex i.e. group 1 was male = 1 0 0, group 2 female = 0 1 0, and group 3 unsexed = 0 0 1. The data contained in the Excel matrix were imported into Notepad++ v6.2 (arranged in a vertical series format i.e. columns = years, rows = individuals) and then exported as a capture history input (.INP) file for further analysis in program MARK version 6.0 (White and Burnham, 1999) in Chapter 5 (see Appendix Table A.1 for individual capture histories).

RESULTS

Dorsal fin images: mark-recapture

During winter months, white sharks were frequently encountered during photo-ID surveys. In total, 1047 dorsal fin images were photographed throughout the entire 53-month sampling period (April 2004–September 2012), which represented live encounters of 372 individual *C. carcharias*. Of the 1047 images, 970 (92.6%) were taken during the 34-month sampling period between May and September each year (see Chapter 4), and were also graded 7 or 8 points. Seventy-seven images (7.4%), representing 69 different individuals were excluded from further analysis; 27 images (2.6%) were taken before May 1 or after September 30, and 50 images (4.8%) were graded $\leq$ 6 points and were thus deemed too poor in quality to be unambiguously matched.

The 970 good quality images contained sufficient data to reliably identify 303 different white sharks (112 male: 111 female: 80 unsexed, giving sex ratio 1.0: 1.0: 0.7). Considered across all 34 months, the greatest number of recaptures was 21 times for a male and 16 times for a female. The longest periods between recaptures were 2479 days for a male and 2270 days for a female. Over the entire study period, both left- and right-hand-side dorsal fin images were photographed for 65% of all sharks (n = 197), with just a single left- or right-hand-side image acquired for 35% (n = 106) of all other sharks in the study. The maximum number of years in which any single shark was photographed was seven out of nine years (Figure 3.9.WS0001).

Repeatability and long-term identification

The photo-ID method was repeatable and reliable, and was used to effectively identify among different white sharks throughout this nine-year study. The method did not require annual visitation of sharks to keep track of any potential differences to fins or their features, which rarely occurred. Overall, dorsal fin profile and fin-tip shape, and the presence, orientation, and size of notches, gouges, spikes and lobes, were remarkably stable and did not change drastically or unidentifiably over time, but varied considerably between individuals (Figures 3.1–3.4). The male "WS0001" was the most frequently encountered shark in the study, first captured in 2004 and last recaptured in 2012; he was encountered in all years except 2008 and 2010 (Figure 3.9

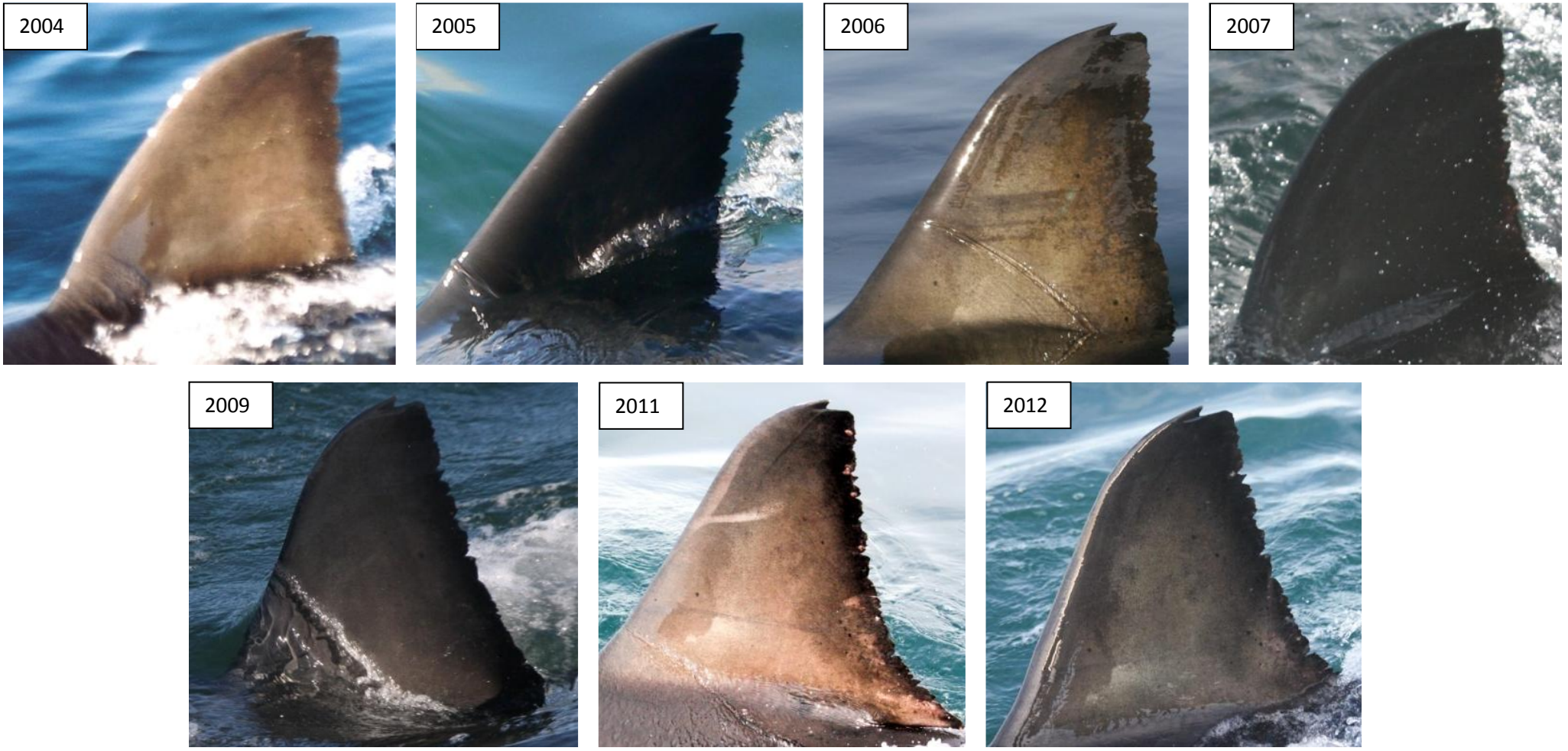

Figure 3.9.Left-hand-side dorsal fin images for a male white shark (WS0001) showing the longevity of natural marks and scars over a nine-year period.

Similarly, long-term visitation has been reported for male sharks to sites off Central California, i.e. 16–22 y (Anderson *et al*., 2011), and Guadeloupe Island (Nasby-Lucas and Domeier, 2012). Images collected for this now mature male spanned nearly a decade, which clearly demonstrated that general shape and structure of his fin, notch positioning and size, black pigment spots and a faint white blemish, as well as a healed scar through the fin tip, which created a spike, were all remarkably stable over approximately one decade (Figure 3.9). However, white pigmentation blemishes and black pigments spots (around or within white blemishes) changed ontogenetically growing respectively less and more conspicuous over time (Figure 3.10). Changes in pigments were taken into consideration when matching images to avoid misidentification. On occasion, features at the base of the dorsal fin, such as white blemishes on the leading edge or notches in the trailing edge, were sometimes obscured by water or completely unidentifiable due to maiming injuries. Fortunately, this was not an insurmountable issue when both natural and auxiliary mark types were conspicuous, and could therefore be used to positively identify individual sharks using a multi-feature search approach (Figure 3.8, WS0226). The keyword system in Lightroom was labour intensive to develop, but the method provided a viable option for matching dorsal fin images reliably and rapidly by comparison to fully manual searches.

DISCUSSION

Although white sharks lend themselves well to surface based photo-ID methods, the viable long-term use of dorsal fin natural marks to identify individual *C. carcharias* has been questioned until recently. Most criticism has focussed on the longevity and stability of the unique trailing edge notch pattern, which provides a morphologically distinct identifying trait for individual white sharks, analogous to a fingerprint for humans (Chapple *et al*., 2011). Domeier and Nasby-Lucas (2007) criticized the use of these features, noting that small or distinguishing marks can easily be erased by fresh, larger marks, which, in their opinion, can create serious problems in long-term monitoring studies. In theory, this would be problematic, but fortunately, in practice, this is rarely a major problem, even once considerable structural damage disfigures a fin, or the trailing-edge is completely bent over, obscured or destroyed, since correct identification is still possible using multiple mark types, both natural and non-natural *auxiliary* features (Figure 3.8). Furthermore, using the combination of mark-types presented in this study, overcomes any potential limitations with

using notches exclusively. The most stable and hence reliable natural feature was the top third of the dorsal fin, as was also reported by Towner *et al*. (2013) for white sharks in Gansbaai.

Gubili *et al*. (2009) demonstrated a high degree of concordance (85%) between matched dorsal fin images and genetic markers, further validating the use of dorsal fins to identify white sharks over periods of at least five years. More recently, Anderson *et al*. (2011) concluded, from a study spanning 22 years, that there was no evidence of long-term changes in size, shape or arrangement of existing notches on white shark dorsal fins (n = 5 individuals), finally stemming any debate on the viable use of dorsal fins and their natural features. The findings of the current study support these conclusions, strongly suggesting that dorsal fin shape and natural marks are reliable, robust, anatomical features, which are remarkably stable and do not change with age, or alter dramatically and unidentifiably over time (Figure 3.9). Thus, photo-ID can be reliably used for long-term monitoring studies on wild populations of these large, enigmatic sharks, even over periods of up to at least 22 years (Anderson *et al.,* 2011), or approximately half of the estimated life-span of *C. carcharias* (Bruce, 2009).

In total, 372 individual *C. carcharias* were identified in this study. However, 69 different individuals were excluded from further analysis, because images were taken outside of the 34 month restricted sampling period (May–September), and/or graded $\leq$ 6 points, and thus were too poor in quality to be matched reliably. As such, 303 white sharks comprised the photo-identified population made up of 112 males, 111 females, and 80 unsexed sharks. The total number of sharks identified, i.e. captures, were lower than numbers identified in Gansbaai (n = 532), but greater than for other aggregation sites in South Africa, such as Bird Island in Algoa Bay (n = 53) (Dicken *et al*., 2013), and Mossel Bay (n = 261) (Ryklief, 2012). By comparison to other populations, overall numbers of sharks identified at Seal Island were higher than numbers off Central California (n = 130) (Chapple *et al*., 2011) and at Guadeloupe Island (n = 113) (Nasby-Lucas and Domeier, 2012; Sosa-Nishizaki *et al*., 2012), which suggests that False Bay has a large number of large white sharks compared to most other well-researched sites worldwide. However, estimates of gross numbers of sharks identified do not provide a suitable indicator of population size, as these estimates do not incorporate probability of capture, which will be presented in Chapter 5 using the POPAN (Schwarz and Arnason, 1996) version of the Jolly Seber model.

Both left- and right-hand-side dorsal fin images were photographed for 65% of all sharks, with just a single left- or right-hand-side image acquired for 35% of all other sharks.

This provides strong grounds for confidence that dorsal fin images were matched accurately, with negligible pseudo-replication and misidentification error, given that the majority of images had a second reference image to confirm matches. Despite the remaining 35% of sharks having just a single-sided image, this was not a limitation, because images had been graded using a similar process to other photo-ID studies (Chapple *et al*., 2011), and were therefore good quality. In addition, all graded images were assessed independently by a second party, in order to account for observer bias. This provided further checks for consistency, and thus increased confidence that individuals were matched accurately. Furthermore, despite certain sharks having skipped a year or several years between capture and recapture events, sharks were successfully matched in the catalogue in later years, even after periods of up to 2479 days between encounters, which demonstrated that the method is repeatable and reliable over extended periods of time. The greatest number of recaptures was 21 times for a male and 16 times for a female, which demonstrates that certain white sharks exhibit strong site-fidelity to Seal Island, and further validates the use of photo-ID at this site.

Ontogenetic changes in body patterning has been reported for leopard and tiger sharks, *Stegostoma fasciatum* and *Galeocerdo cuvier* respectively (Dudgeon *et al*., 2008; Last and Stevens, 2009), but not for other elasmobranchs, such as *Manta alfredi*, which clearly demonstrates long-term stability of body-markings in some species (Marshall *et al*., 2011). No ontogenetic changes are known to affect white shark dorsal fin structure, general integrity or colouration. However, direct evidence in the current study demonstrated that ontogenetic changes do occur with dorsal fin pigments i.e. black spots darkened, widened and became more prominent within white pigmentation blemishes, which, alternatively and conversely might have faded, over short time periods < 3 years (Figure 3.10). Towner *et al*. (2013) recently reported changes in dorsal fin pigments for white sharks in Gansbaai, which suggests the phenomenon is not restricted to this one example. However, this remains to be tested comprehensively (i.e. frequency of occurrence and whether changes are sex-related), which provides an avenue for further research. While misidentification from pigments does not create a serious problem, it highlights the importance of avoiding single-feature search approaches, especially searches based solely on pigments as standard search criteria, which were therefore avoided.

Future regional studies on white sharks would benefit from using the photo-cataloguing protocol described, particularly to hasten searches for recaptures. This approach can be used as a reliable alternative until automated recognition software programs become available, which incorporate acceptable levels of data waste. Similar to the findings of the

current study, Chapple *et al*. (2011) attempted to use the program DARWIN to catalogue white shark dorsal fins, but found unacceptable levels of error, whereas Towner *et al*. (2013) successfully used the program. Photo-ID studies on other elasmobranchs have also reported limitations with data waste using similar automated software programs (Kitchen-Wheeler, 2010; Marshall *et al*., 2011). Irrespective of the search process used to differentiate among photographs, images are always likely to be accepted or rejected visually. Thus, observer input is essential and is unlikely to be removed from the identification process entirely, even with automated software.

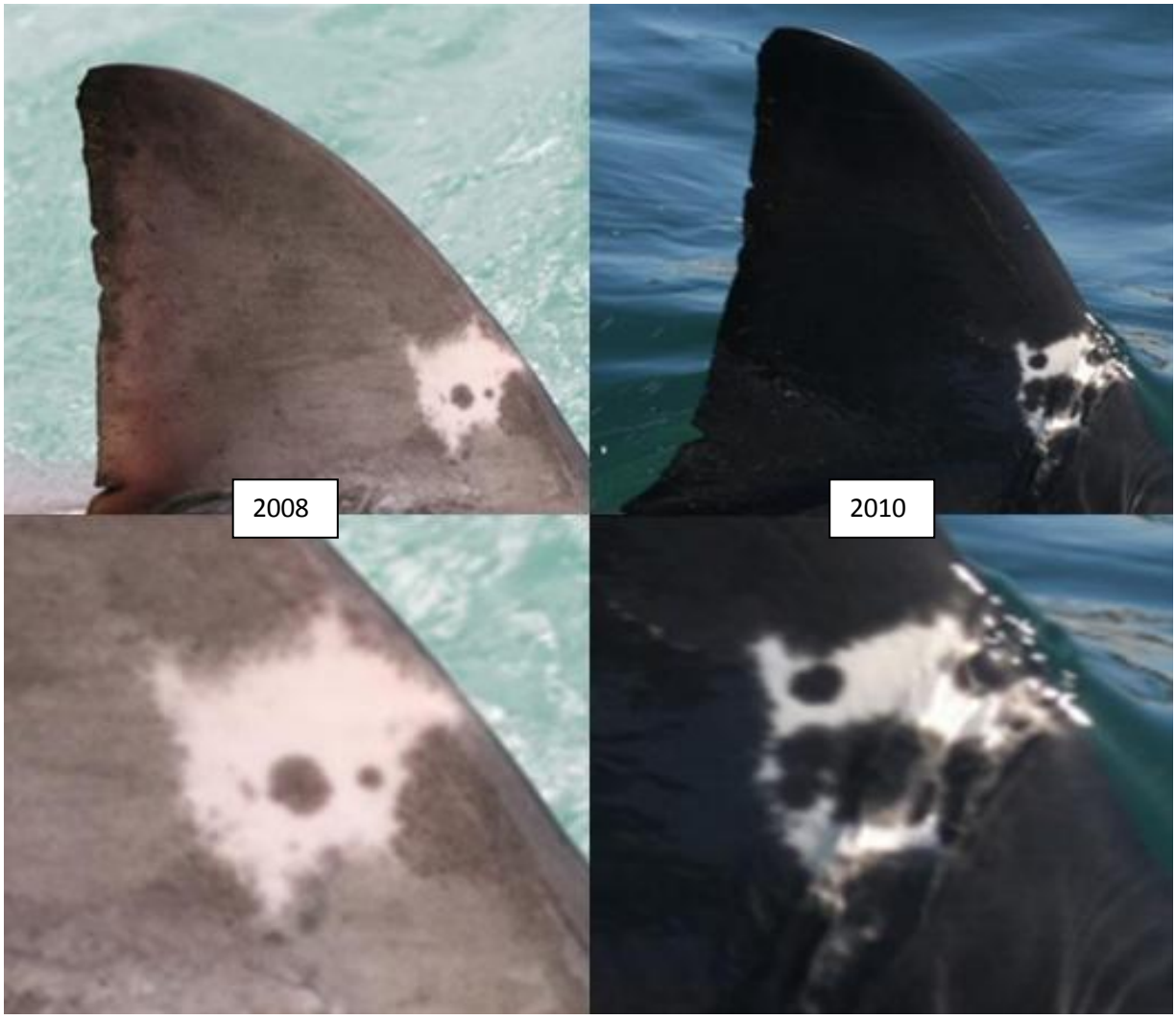

Figure 3.10.An example of ontogenetic change in dorsal fin pigmentation of an adolescent (~250–300 cm) male white shark (WS0265) photographed in Gansbaai in 2008 and at Seal Island in 2010.

While keyword filtering is viable for localised photo-ID studies at discrete aggregation sites with relatively small sample sizes, this approach would be restrictively laborious for a national study, which might incorporate thousands, if not tens of thousands, of

images from multiple aggregation sites. Thus, a national study would benefit greatly from using automated software, regardless of data waste. Photo-ID is an extremely valuable and powerful tool that provides a suitable platform to assess white shark population dynamics on regional, national and international scales, and could be applied to assess rates of mixing and emigration between aggregation sites within South Africa, or between populations in South Africa and Australia (Bonfil *et al*., 2005). A national study would be hugely beneficial for white shark conservation in southern Africa and would assist with more precise, robust estimates of population size, as well as other vital demographic rates, such as survival and mortality.

RESEARCH RECOMMENDATIONS

Consistent effort across seasons and high intensity sampling with current photo-ID methods would benefit future demographic research on white sharks at Seal Island. Body pigment-patterns were photographed for white shark gills, pelvic and caudal fins starting in 2011 using GoPro2 digital cameras in underwater (UW) housings (via the method of Domeier and Nasby-Lucas, 2007). Inspection of UW images increased ability to ascertain sex reliably (except in very poor visibility < 2 m and/or with small sharks < 250 cm), which was often difficult to assess from surface-based observations. In addition, laser-photogrammetry was used in conjunction with UW images to develop an accurate total length estimation technique, which holds potential, but is dependent on water clarity. Size estimates could be used to model life-history stage(s) as individual covariates in further mark-recapture population modelling attempts (see Chapter 5) and might also be applied to assess growth rates, although the absolute accuracy of the method is questionable in this regard. Therefore, it is recommend that surface- and underwater-based photographs be collected and laser-photogrammetry be used as routine field operating procedure in further field research, not only to assist with identifying sex and estimating shark size effectively, but to develop a catalogue of body pigment patterns to complement ongoing photo-ID research and thereby ultimately identify as many white sharks as possible at this site. In addition, white shark cage-diving ecotourism operations (n = 3) are present throughout all months of the aggregation at Seal Island, their presence is largely dictated by shark occurrence. In addition, cage diving operators are present in all months of the year in Gansbaai (n = 8) and Mossel Bay (n = 1).

Therefore, public participation via ecotourism ventures, or by ecotourism operators themselves, present a vast and beneficial resource to supplement current photo-ID research.

Furthermore, acoustic telemetry techniques should be used in conjunction with photo-ID, as the combination would be particularly powerful and could be used to assess efficiency of photo-ID at elucidating shark residency times, and the actual extent to which transience occurs (see Chapter 4), or to which sharks are simply not detected with surface based photo-ID techniques. Thus, using behavioural telemetry would assist in identifying limitations with photo-ID, knowledge that could then be applied and accounted for in further mark-recapture studies, which is especially important for robust estimation of survivorship and abundance (see Chapter 5).

To more fully understand the demography and population size of white sharks in South Africa, a consolidated photo-ID database is required. It would be beneficial to include images for both dorsal fins and body pigment patterns collected from all well-studied aggregation sites i.e. False Bay, Gansbaai, Mossel Bay and Algoa Bay. It would also be beneficial to collect images as they become available for catches of large white sharks from other regions of Africa and the Western Indian Ocean i.e. Mozambique, Madagascar, Kenya, Mauritius, Reunion, the Seychelles and the Chagos Archipelago, which can be compared to existing catalogues or a national catalogue, once one has been developed. Long-term collection of images from finning events in Mozambique (e.g. Figure 1.1) and catches in the KZN nets will likely prove valuable in assessment of anthropogenic mortality on survival rates of white sharks in southern Africa, which was highlighted in the current study. An unsexed and unsized shark "WS0185" was photographed on one occasion at Seal Island in 2010, which, unfortunately, was caught dead in the nets in KZN in 2012, and ultimately identified as a male ~350 cm TL (ANS10008 KNZSB reference unpublished data 2012). Photo-ID can be used to assess white shark demographics and manage populations on regional, national, and international scales, and will likely prove a valuable tool in assessing rates of anthropogenic mortality as catalogues become amalgamated into a national white shark photo-ID database.

CHAPTER 4

DEMOGRAPHIC STRUCTURE OF WHITE SHARKS AT A SEASONAL AGGREGATION SITE

INTRODUCTION

White sharks (*Carcharodon carcharias*) aggregate around Seal Island, False Bay, exhibiting a distinct seasonal rhythm, with male and female sharks arriving in autumn and dispersing by spring (Kock *et al*., 2013). Shark occurrence coincides with the increased availability of inexperienced, juvenile Cape fur seal prey (*Arctocephalus pusillus*), with defined peaks in predatory activity of sharks occurring between May and August over winter months (Hammerschlag *et al*., 2006), which suggests that Seal Island is an important, seasonal foraging ground for white sharks. Multiple other studies have shown that aggregations of large white sharks form in response to seasonal availability of juvenile pinniped prey, with arrival times of sharks coinciding with prey availability at different sites (Ainley *et al*., 1985; Martin *et al*., 2005; Bruce *et al*., 2005; Kock and Johnson, 2006; Robbins and Booth, 2012; Kock *et al*., 2013). However, while pinniped prey appears to be one underlying motivating factor responsible for regulating white shark occurrence at these sites, the seasonality, sex ratio, size distribution and maturity composition and behaviours of sharks, differ markedly between sites, suggesting that predation might just be one important regulating factor.

White shark size distribution correlates well with longitude along the South African coast. Shark total length (TL) generally decreases from west to east coasts, such that shark TL in False Bay > Gansbaai > Mossel Bay > Algoa Bay > KZN (Cliff *et al*., 1996a; Ferreira and Ferreira, 1996; Kock and Johnson, 2006; Dicken, 2008; Dudley, 2012; Ryklief, 2012; Dicken *et al*., 2013), a pattern similar to that observed in US shark populations (Casey and Pratt, 1985; Klimley, 1985). Therefore, False Bay has one of the largest proportions of large white sharks (> 400 cm TL) that are regularly encountered in South Africa (Kock and Johnson, 2006), although large and potentially mature females (> 470 cm TL) are rarely encountered. Ferreira and Ferreira (1996) attributed low frequencies of large sharks in the Western Cape to intense hunting pressure in the three decades preceding their study (T. Ferreira personal comm. cited by Cliff *et al*., 1996a), but it seems more likely that this size class of white shark rarely occurs in coastal waters of South Africa (Dudley, 2012).

Size segregation has been reported for white sharks in KwaZulu-Natal (KZN) (Cliff *et al*., 1989, 1996a) and Algoa Bay (Dicken, 2008), but not at other aggregation sites, such as Mossel Bay (Ryklief, 2012), Gansbaai (Ferreira and Ferreira, 1996) and False Bay (Kock *et al*., 2013). Available evidence suggests that the intermediary Eastern Cape section of coastline may serve as a pupping ground (Cliff *et al*., 1989), with inshore areas of Algoa Bay having been proposed as a nursery area for young-of-the-year (YOY) and juvenile white sharks (Cliff *et al*., 1989, 1996a; Dicken, 2008). Mossel Bay has been proposed as an interim nursery "grow-out" area, where juvenile white sharks can forage on a diverse range of elasmobranch, teleost and marine mammal prey, attain larger sizes with less intraspecific competition from larger conspecifics, and can thus grow out of adolescence before moving west to Gansbaai and False Bay (Ryklief, 2012), where large white sharks frequently predate on fur seals in winter months (Hammerschlag *et al*., 2006; Kock *et al*., 2013).

Differing requirements or preferences of life-history stages and sexes for optimum water temperatures and/or preferred prey species influences the distribution of white sharks (Domeier, 2012; Robbins and Booth, 2012). Tricas and McCosker (1984) proposed that white shark diet changed ontogenetically from one dominated by teleost and elasmobranch prey (< 300 cm TL) to one dominated by marine mammals (> 300 cm TL), due to the high energetic demands associated with increasing body size (Semmens *et al*., 2013). In South Africa, white shark movements are thought to be mediated through intraspecific competition, but driven by ontogenetic size-based prey selection (Hussey *et al*., 2012; Smale and Cliff, 2012). Thus, it seems probable that different sites along the coast accommodate different biological and/or environmental requirements that assist with foraging, refuge or reproductive behaviours for various life history stages. The result is longitudinal distribution by size and a seasonal shift of maturing white sharks into Western Cape waters.

Despite these studies, no long-term demographic data are available for the aggregation white sharks at Seal Island. Therefore, Chapter 4 presents a demographic analysis with inter-annual and inter-monthly trends in effort, shark sighting frequencies, sighting rate analyses (SPUE) and sex ratios for the period 2004–2012. In addition, dorsal fin image mark-recapture data are used to assess annual captures and recaptures, to identify residents and transients, assess site-fidelity of sexes, frequencies of immigration and emigration and the size distribution and maturity composition of the population. This study might arguably present some of the most vital information to date in terms of reproductive stock assessment and reveals further insights into biology, behaviour and life history of white sharks in South Africa.

MATERIALS AND METHODS

Data available

The white shark aggregation at Seal Island was monitored each year between 2004 and 2012; a 53-month period, from February to October, which comprised 268 „routine" sighting surveys conducted over 992.91 hours (see Chapter 3 for survey methods). A preliminary inspection of effort hours and shark sighting frequencies identified May–September as the peak five-month period when shark and research activity were both highest and most consistent. Of the 268 routine surveys, 92% (n = 247) took place in May–September each year, that encompassed a total period of 45 months (5 months × 9 years). Of the 45 months, 11 were excluded from further analysis because sharks were not sighted in one month (September 2006) and ten of the months were not surveyed due to logistical constraints. This resulted in a total of 34 months of sampling with usable data. All data collected between October 1 and April 30 of the following year, and sightings data from any routine survey in any month without photo-ID effort, were excluded from further analysis. This included the earliest arrivals (January–April) and latest departures (October–December) of sharks from the seal colony, when sampling effort was negligible in most years. Only those data (i.e. effort hours, shark sightings and dorsal fin images) collected within the restricted 34-month period and within photo-ID surveys only (i.e. those routine surveys when photographs were collected) were further used to examine and describe in detail the demographics of white sharks at Seal Island.

Effort hours and sightings were pooled (independently) by calendar month, within and across years, respectively, and plotted graphically to assess inter-annual and inter-month trends and potential relationships. Pooled annual and monthly numbers of sightings and hours were used to derive an index of relative shark abundance (expressed as sharks per hour, sighting rate or SPUE) using sightings per unit effort analyses. Sex ratios were derived from sightings data for years and months and were used to assess sex-specific inter- and intra-seasonal trends.

Numbers of captures and recaptures were quantified from dorsal fin image mark-recapture data, to determine the proportion of residents (sharks recaptured in at least one other year) and transients (sharks captured in one year only) to assess rates of permanent and temporary emigration. Transients are defined as being marked and released, followed by immediate and permanent emigration from the study area, whereas, residents are defined as being marked and released, and then conditional on surviving between sampling occasions, they return and are available for recapture in a subsequent sampling period with estimable

probability. Ratios of recaptures to new captures were plotted graphically to further identify periods of recruitment, immigration and emigration, and a direct comparison was made for total numbers of sharks sighted against either photo-identified (captures + recaptures) or sighted but photographically unidentified, to gauge photo-ID efficiency.

All mark-recapture events (i.e. captures and recaptures) for which total length (TL) estimates were reliably acquired were pooled into 49 cm size classes and the size frequency distribution and maturity composition were assessed for the photo-identified population. Maturity classes were defined separately for sexes, with immature, subadult and mature males defined at 150–299, 300–349 and >350cm TL respectively, and females at 150–399, 400–449 and > 450cm TL respectively. Maturity composition was not assessed for unsexed sharks, nor males and females without TL estimates, given that maturity status could not be ascertained without sex and/or TL information.

Statistical analysis

Inter-annual and inter-monthly trends in mean sightings rates (SPUE) were assessed for the "sighted" population and for each sex independently to describe both long-term and intra-seasonal trends and/or changes in white shark activity patterns at Seal Island. Data were analysed with a two-way ANOVA with main effects for sex, year, and month, with an interaction of year and sex (e.g.$\mathrm{SPUE} \sim \mathrm{month} + \mathrm{sex} + \mathrm{year} \times \mathrm{sex}$) (Thaka and Gentleman, 1996). Post-hoc differences in means were assessed with a Tukey"s test. For analysis of sex ratios, a log-linear model was used to assess the independence of counts by sex, year and month. Chi-square tests were used to assess sex differences in recapture frequencies, and both the size distribution and maturity composition of the photo-identified population.

RESULTS

Overview: Routine and photo-ID survey effort

Of the 268 routine surveys, 247 took place between May and September each year, with only 21 surveys (8%) conducted between October 1 and April 30 of the following year. These were excluded from further analysis (Figure 4.1). A comparison of hours spent during routine and photo-ID surveys in May–September showed considerable loss of data in 2004 and 2005, both in terms of effort hours and sightings, because photo-ID effort was minimal over this period. Photo-ID hours comprised 12% and 50% of routine hours spent between May and

September in 2004 and 2005 respectively. In 2006 and 2007, photo-ID hours were similar to routine hours that comprised 84% and 88% of the data, respectively. In 2008, only 46% of routine surveys hours were spent photographing white sharks. The magnitude of the difference in effort was reduced in later years, when photo-ID sampling effort increased between 2009 and 2012, fully saturating routine surveys in 2009, 2011, and 2012, with approximately 78% effort saturation in 2010. Thus, disproportionally low photo-ID effort in 2004 and 2005 resulted in a large amount of sightings and effort data being excluded from further analysis, whereas in mid-late years photo-ID and routine hours were less disproportionate by comparison and the majority of data were included in the analyses.

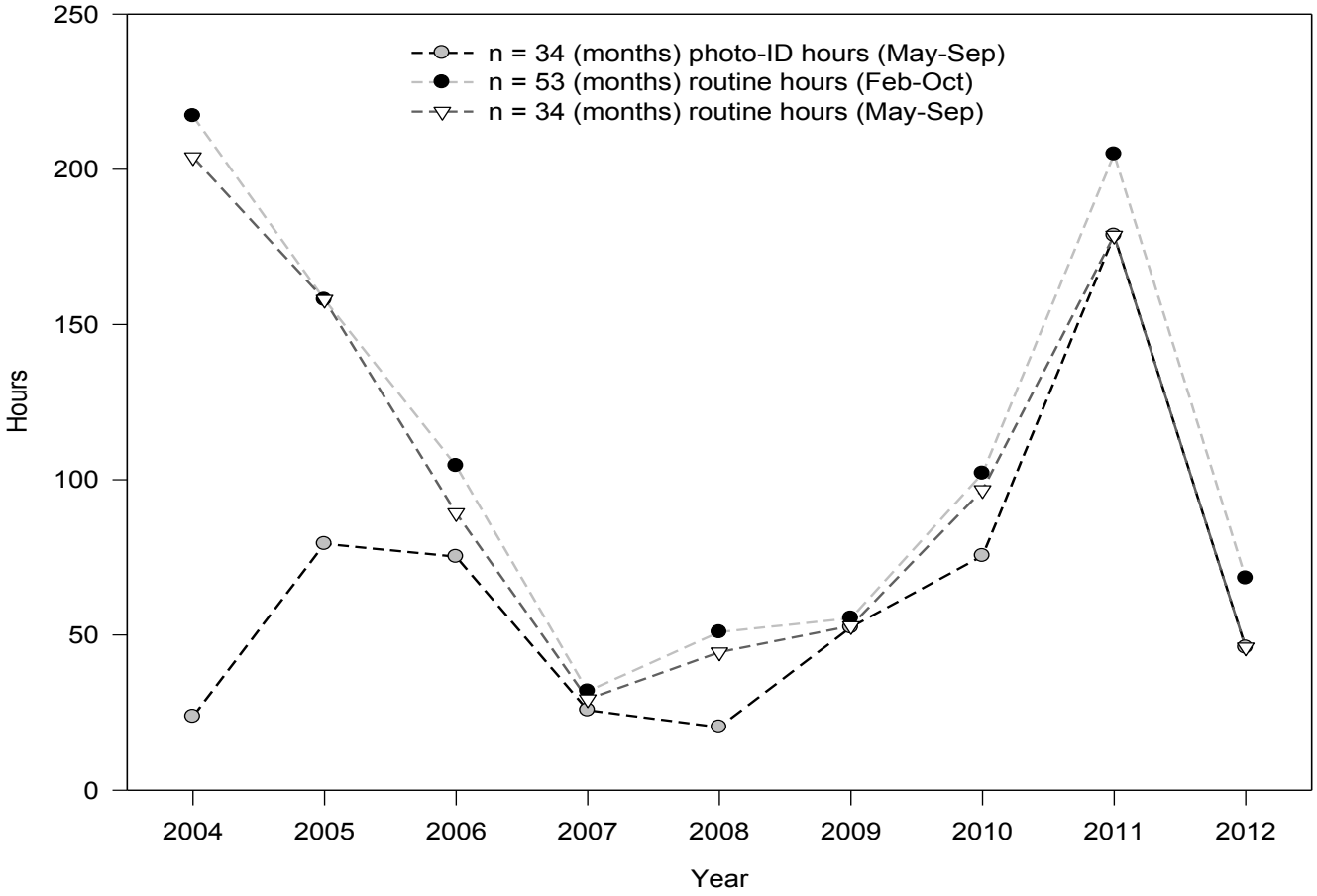

Figure 4.1.Inter-annual comparison of effort hours spent in routine surveys in February–October, with both routine and photo-ID effort hours spent in May–September each year at Seal Island.

Of the 247 routine surveys conducted in May-September, both shark sightings data and dorsal fin images were collected during 171 "photo-ID surveys" or approximately 70% of routine surveys. Photo-ID effort hours and shark sightings, SPUE sighting rates and sex ratios based on sightings data are summarised for years and months (Table 4.1) for the sighted population and for each sex independently. These data form the foundation for all further analyses presented in Chapter 4 (except dorsal fin mark-recapture; see Chapter 3).

Table 4.1.Summarised annual and monthly numbers of effort hours and shark sightings, with sharks per hour (SPUE) and sex ratios for the population of white sharks sighted during photo-ID surveys (n = 171) conducted at Seal Island each year (2004–2012) between May and September (n = 34 months) (SE = standard error values, N = number of sightings, ♂ = male, ♀ = female, *U* = unsexed).

Annual										
	Survey	N	N	N	N	SPUE Population	SPUE ♂	SPUE ♀	SPUE *U*	Sex ratio
Year	hours	Population	♂	♀	*U*	mean (SE)	mean (SE)	mean (SE)	mean (SE)	(♂: ♀: *U*)
2004	23.71 (2.97)	27	8	5	14	1.09 (0.28)	0.35 (0.06)	0.22 (0.08)	0.52 (0.42)	(1.5: 1.0: 1.7)
2005	79.34 (8.21)	259	87	99	73	2.78 (0.72)	0.91 (0.27)	1.20 (0.17)	0.67 (0.36)	(0.7: 1.0: 0.5)
2006	75.19 (5.85)	210	46	27	137	3.19 (0.43)	0.58 (0.28)	0.33 (0.14)	2.28 (0.53)	(1.8: 1.0: 5.8)
2007	25.75 (1.72)	52	15	27	10	1.94 (0.42)	0.53 (0.11)	1.14 (0.37)	0.27 (0.17)	(0.5: 1.0: 0.2)
2008	20.27 (1.19)	40	10	19	11	2.08 (0.51)	0.53 (0.23)	0.82 (0.25)	0.73 (0.43)	(0.5: 1.0: 0.7)
2009	52.49 (3.59)	86	21	22	43	1.34 (0.51)	0.31 (0.16)	0.32 (0.15)	0.70 (0.27)	(0.7: 1.0: 2.9)
2010	75.48 (6.99)	146	51	41	54	1.71 (0.47)	0.63 (0.29)	0.43 (0.15)	0.66 (0.13)	(1.3: 1.0: 2.3)
2011	178.69 (9.97)	199	78	48	73	0.90 (0.21)	0.34 (0.11)	0.25 (0.04)	0.32 (0.09)	(1.2: 1.0: 1.0)
2012	46.00 (3.29)	86	13	18	55	1.83 (0.34)	0.23 (0.14)	0.31 (0.13)	1.29 (0.24)	(0.6: 1.0: 4.2)
Mean	64.1	123	37	34	52	1.87	0.49	0.56	0.83	(1.0: 1.0: 2.3)
Total	576.92	1105	329	306	470					
Monthly										
	Survey	N	N	N	N	SPUE Population	SPUE ♂	SPUE ♀	SPUE U	Sex ratio
Month	hours	Population	♂	♀	*U*	mean (SE)	mean (SE)	mean (SE)	mean (SE)	(♂: ♀: *U*)
May	71.78 (4.27)	121	16	27	78	1.88 (0.57)	0.37 (0.18)	0.62 (0.40)	0.89 (0.41)	(0.5: 1.0: 2.1)
Jun	141.78 (4.69)	367	124	105	138	2.21 (0.46)	0.71 (0.18)	0.56 (0.15)	0.94 (0.26)	(1.3: 1.0: 1.6)
Jul	168.30 (5.86)	345	120	81	144	2.31 (0.25)	0.61 (0.10)	0.56 (0.15)	1.14 (0.38)	(1.1: 1.0: 1.7)
Aug	160.31 (5.94)	232	65	79	92	1.61 (0.29)	0.40 (0.12)	0.62 (0.18)	0.60 (0.14)	(0.6: 1.0: 1.1)
Sep	34.75 (1.62)	40	4	14	18	0.84 (0.22)	0.11 (0.05)	0.33 (0.11)	0.40 (0.18)	(0.5: 1.0: 1.0)
Mean	115.38	221	66	61	94	1.77	0.44	0.54	0.79	(0.8: 1.0: 1.5)
Total	576.92	1105	329	306	470					

Temporal variation in effort hours and shark sighting frequencies

Annual trends

During 171 photo-ID surveys, 576.92 hours were spent observing and identifying white sharks and photographing dorsal fins. In total, 1105 individual sightings were recorded (329 ♂, 306 ♀, 470 *U*) (Table 4.1, Figure 4.2).

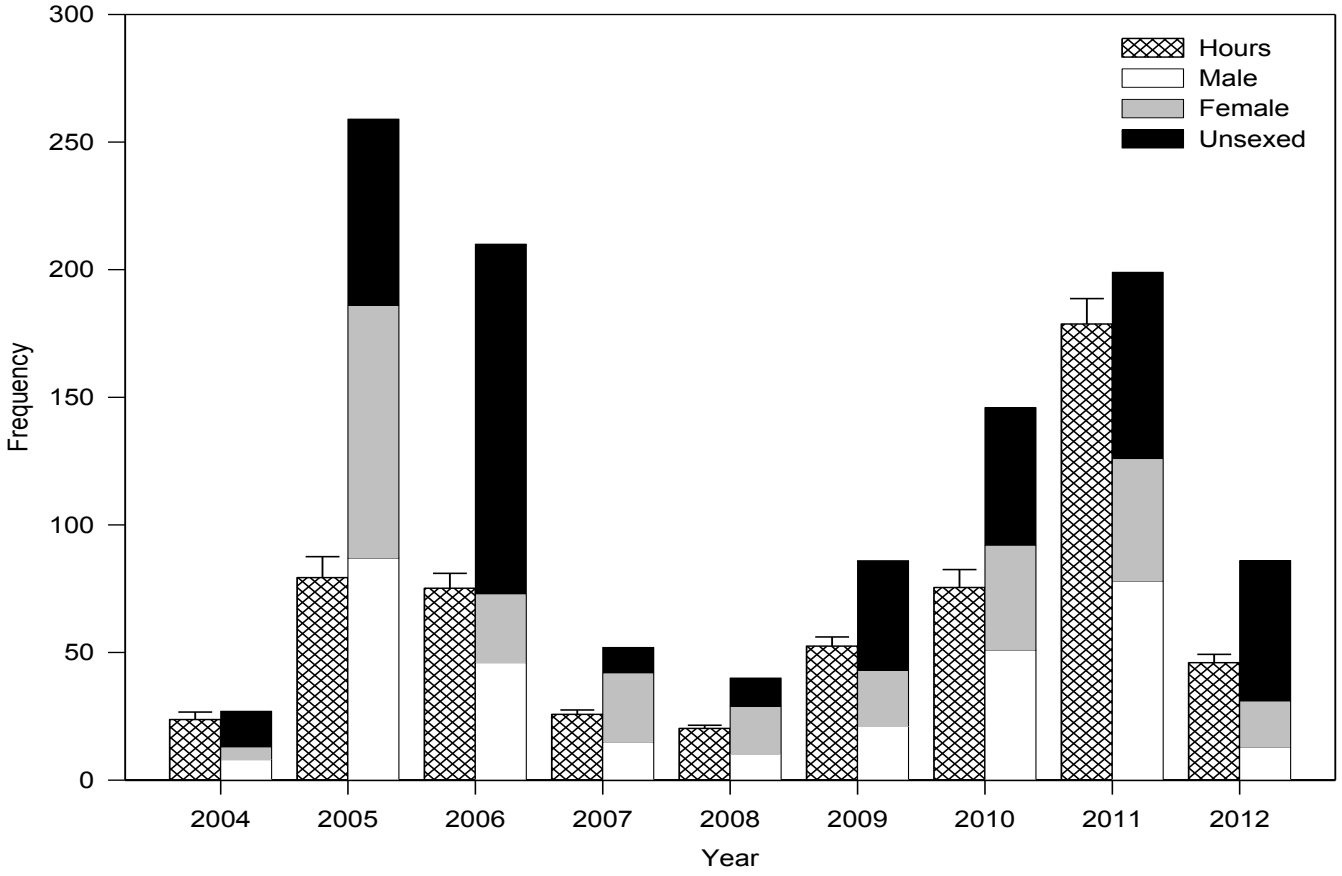

Figure 4.2.Inter-annual comparison of total effort hours spent and sighting frequencies of white sharks at Seal Island by sex. Bars represent standard errors.

Few sharks were sighted in 2004 because photo-ID effort was low, but an increase in effort in 2005 and 2006 dramatically increased sighting frequencies. June and August in 2005 and 2006 represented the only two months and years when > 20 sharks were sighted in single survey(s), with a maximum of 36 individuals sighted in any one survey (10/06/05). Effort and sighting frequencies both decreased in 2007 and 2008, then increased slightly in 2009, but were still both moderate-low compared to most other years. Effort increased in 2010 and reflected hours spent in both 2005 and 2006, which resulted in a substantial increase in sightings, although frequencies were lower in 2010 than in 2005/2006. Sightings increased in

2011 to reflect frequencies in 2005/2006, but effort was 2.3 (2005) and 2.4 (2006) times greater in 2011 and fewer sharks were sighted than expected. Effort and sightings declined in 2012 and both resembled effort and sightings in 2009.

In general, effort was low and variable at the beginning of the study, and then increased in mid-later years, with more consistent photo-ID sampling. Sharks were particularly abundant and sightings were highest in earlier years, when effort was lowest and inconsistent, whereas sightings in later years were lower than expected, given that effort was particularly high and sampling was efficient. This strongly suggests a general decline in abundance and occurrence of white sharks at Seal Island between 2004 and 2012.

Monthly trends

On average, effort hours increased each year from May, in late-autumn, to reach a peak over winter months. Hours spent were highest in July (mid-winter), followed closely by August (late-winter) and then June (early-winter), with a vast reduction in September with the onset of spring (Table 4.1, Figure 4.3).

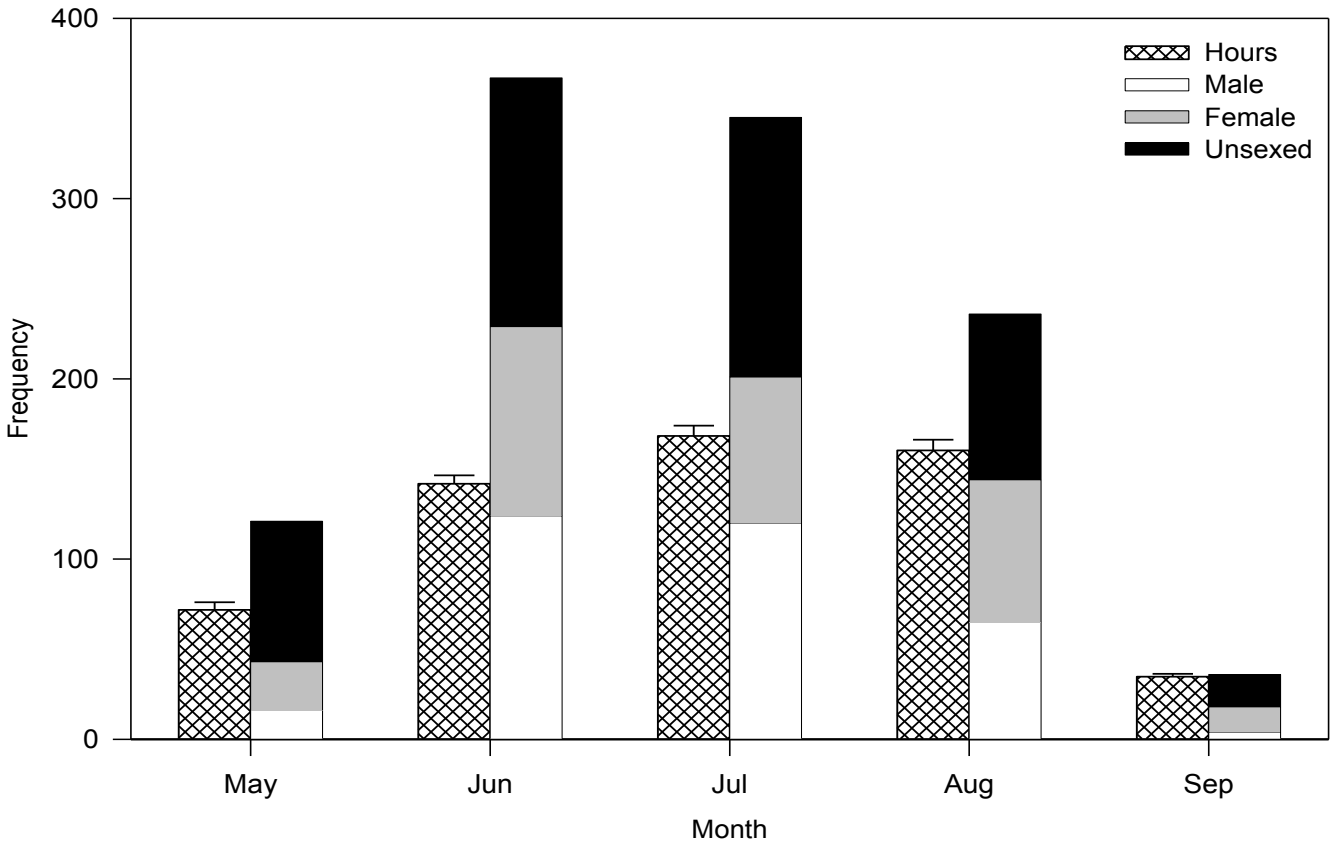

Figure 4.3.Inter-monthlycomparison of total effort hours spent and sighting frequencies of white sharks at Seal Island by sex. Bars represent standard errors.

Similarly, sighting frequencies increased each year from May over the winter and declined by September. However, although effort was highest in July and August, sighting frequencies were highest in June, followed closely by July, and then declined in August. This was despite similar hours of effort being spent during each of the three winter months on average. Effort was greater in August than June, suggesting that sharks were less abundant and had started to disperse from Seal Island during late-winter, which was consistent with lowest sighting frequncies in September, when sharks had all but dispersed, bringing field work to a close until the following autumn.

Temporal variation in relative abundance *(sighting rates–SPUE)*

Statistical analyses: significant estimates

Significant main effects of year ($F = 3.53$, $df = 8$, $p < 0.01$), month ($F = 3.59$, $df = 2$, $p < 0.01$), and sex ($F = 6.21$, $df = 2$, $p < 0.01$), and a highly significant interaction effect of sex and year ($F = 3.92$, $df = 16$, $p < 0.001$) on mean sighting rates was noted. Post-hoc tests confirmed significant differences between 2006 and 2004 ($p = 0.01$), and 2006 and both 2009 ($p = 0.02$) and 2011 ($p < 0.01$) (Figure 4.4). Significant differences were noted between mean annual sighting rates of unsexed sharks and both males ($p < 0.01$) and females ($p = 0.02$). Mean sighting rates of unsexed sharks differed significantly in 2006 compared to unsexed sharks in all other years ($p < 0.01$), except 2012 ($p > 0.05$), with differences highly significant for 2007 and 2011 ($p < 0.001$), when unsexed sharks were sighted infrequently by comparison. The sighting rate of unsexed sharks in 2006 was significantly higher than for males and females in all years ($p < 0.001$), except females in 2005 ($p > 0.05$) and 2007 ($p = 0.10$). Differences were least significant for unsexed sharks and males in 2005 ($p = 0.02$) and 2010 ($p < 0.01$) (Figure 4.5). Post-hoc tests confirmed significant differences in mean sighting rates in September and both June ($p = 0.02$) and July ($p = < 0.01$), but no significant differences between rates in August and June or July ($p > 0.05$) (Figure 4.6).

Sighting rates: annual trends (SPUE)

The $AMA_{population}$ (Annual Mean Average) sighting rate was 1.87 (range 0.90–3.19) sharks per hour, which was highest in 2006 and lowest in 2011 (Table 4.1, Figure 4.4). Sighting rates were low in 2004, but peaked in 2005 and 2006 to the highest rates documented for all years in the study. The rate then declined in 2007 and remained low in later years (1.34–2.08

sharks h^{-1}). Sighting rates in 2005–2008 and2009–2012 were respectively greater and lower than the $AMA_{population}$ rate of the study, demonstrating a clear decline in shark activity. From an analytical standpoint, however, effort hours spent in 2011 were disproportionately high compared to all other years (e.g. 2.8 times higher than the annual mean of 64.10 h), which may have exacerbated the decline in SPUE rates in 2011. However, field observations noted 2005 and 2006 as especially good years, while 2011 was a particularly poor year for shark activity, which support this general decline in sighting rates.

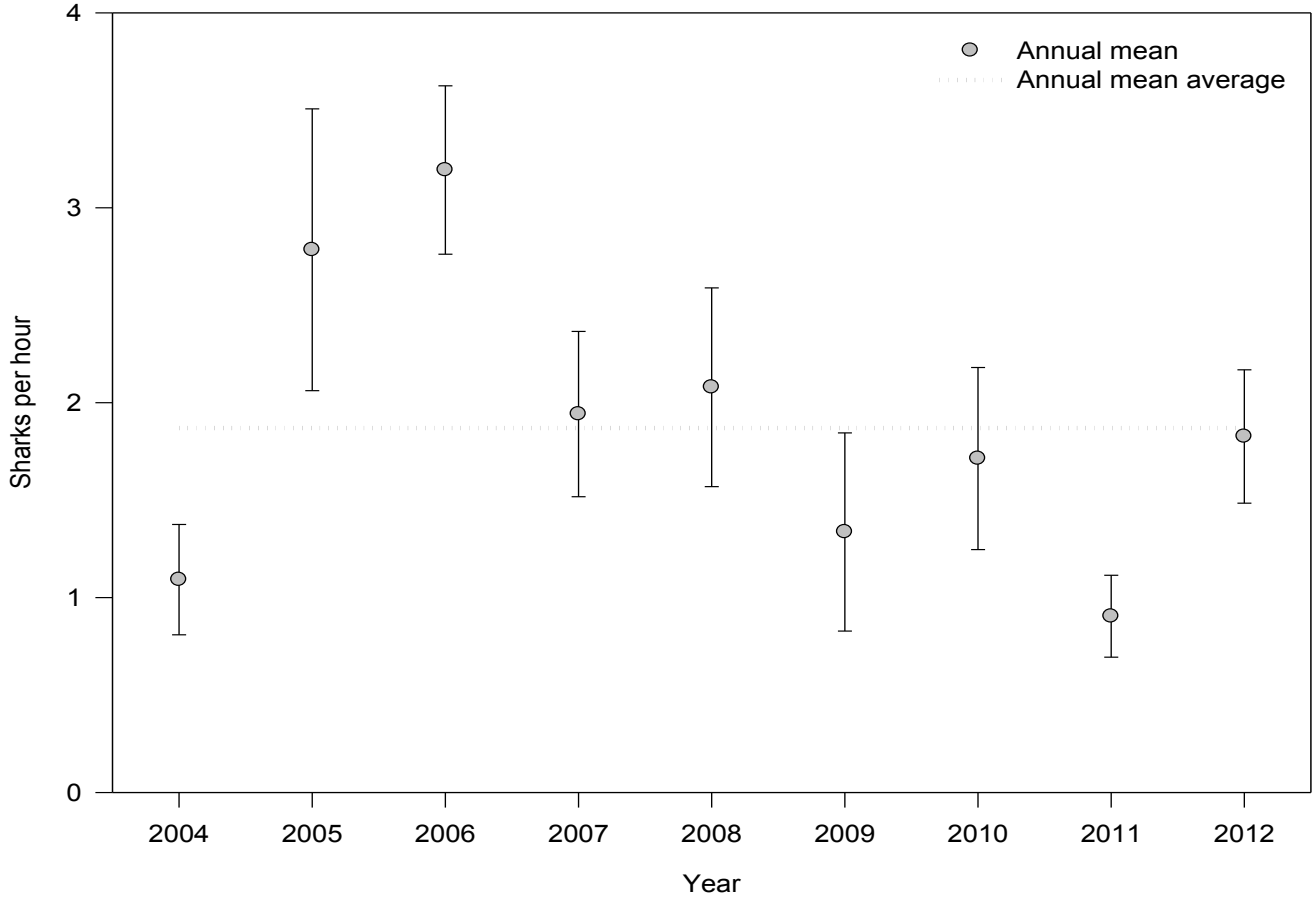

Figure 4.4.Inter-annual comparison of population sighting rates for white sharks at Seal Island. Bars represent mean standard errors.

The AMA_{male}, AMA_{female}, and $AMA_{unsexed}$ shark sighting rates were 0.49 (♂ range 0.23–0.91), 0.56 (♀ range 0.22–1.20) and 0.83 (*U* range 0.27–2.28) sharks per hour, respectively (Table 4.1, Figure 4.5). Male sighting rates peaked in 2005, then decreased consistently with each consecutive year over the duration of the study, with one anomalous peak in 2010 (Figure 4.5). Female sighting rates were highest in 2005, 2007, and 2008, lowest in 2011, and slightly higher than for males overall (Figure 4.5). From 2009 female sighting rates decreased below the AMA_{female} rate and remained persistent and especially low,

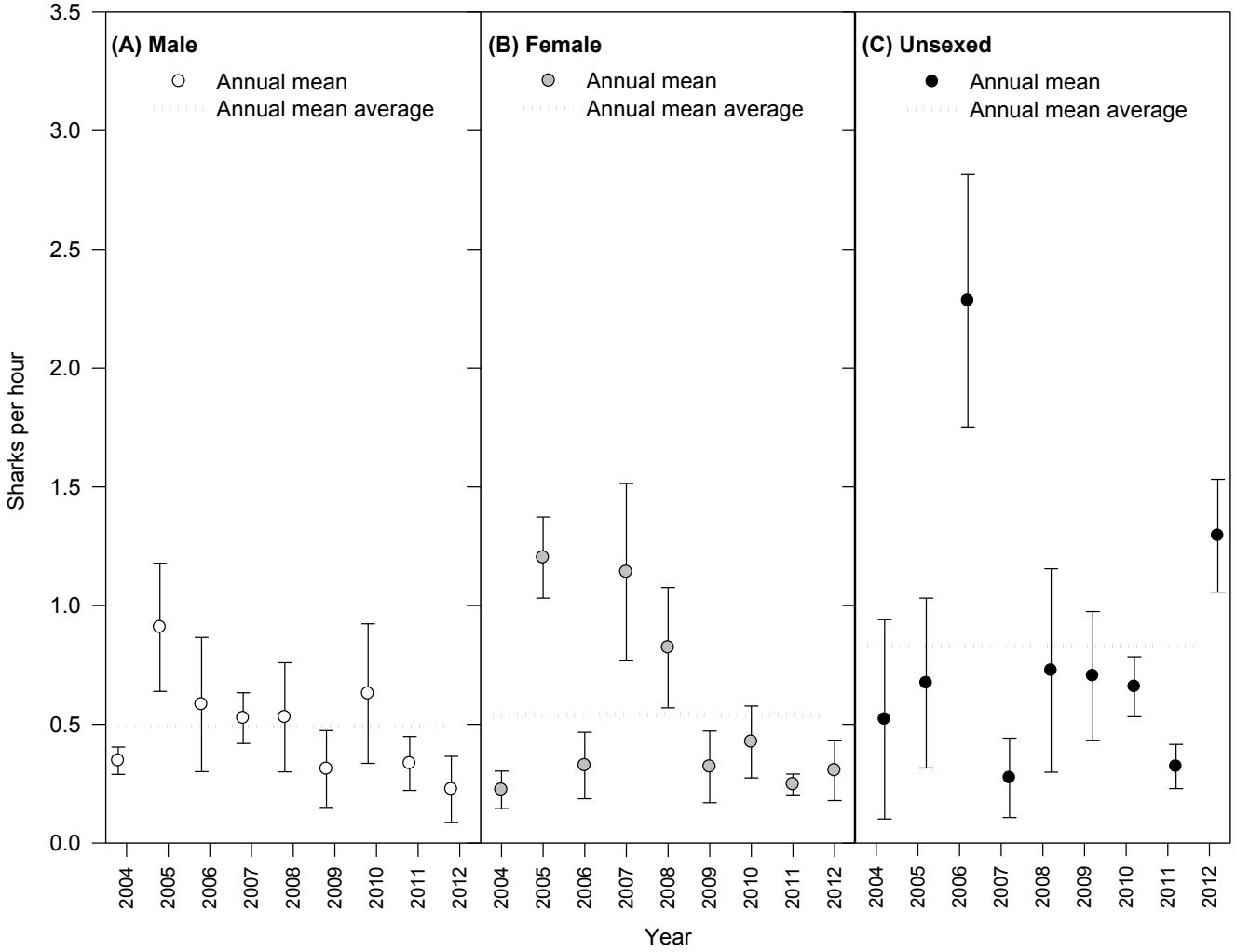

Figure 4.5.Inter-annual comparison of mean sighting rates for male, female and unsexed white sharks at Seal Island. Bars represent mean standard errors.

Sighting rates: monthly trends (SPUE)

The $MMA_{population}$ (Monthly Mean Average) shark sighting rate was 1.77 (range 0.84–2.31) sharks per hour (Table 4.1, Figure 4.6). SPUE increased each year from May to reach a maximum over June and July and declined over August into September. SPUE in May, June

and July, and in August and September, were respectively > and < than the $MMA_{population}$ rate. Sighting rates were significantly lower in spring than in winter months

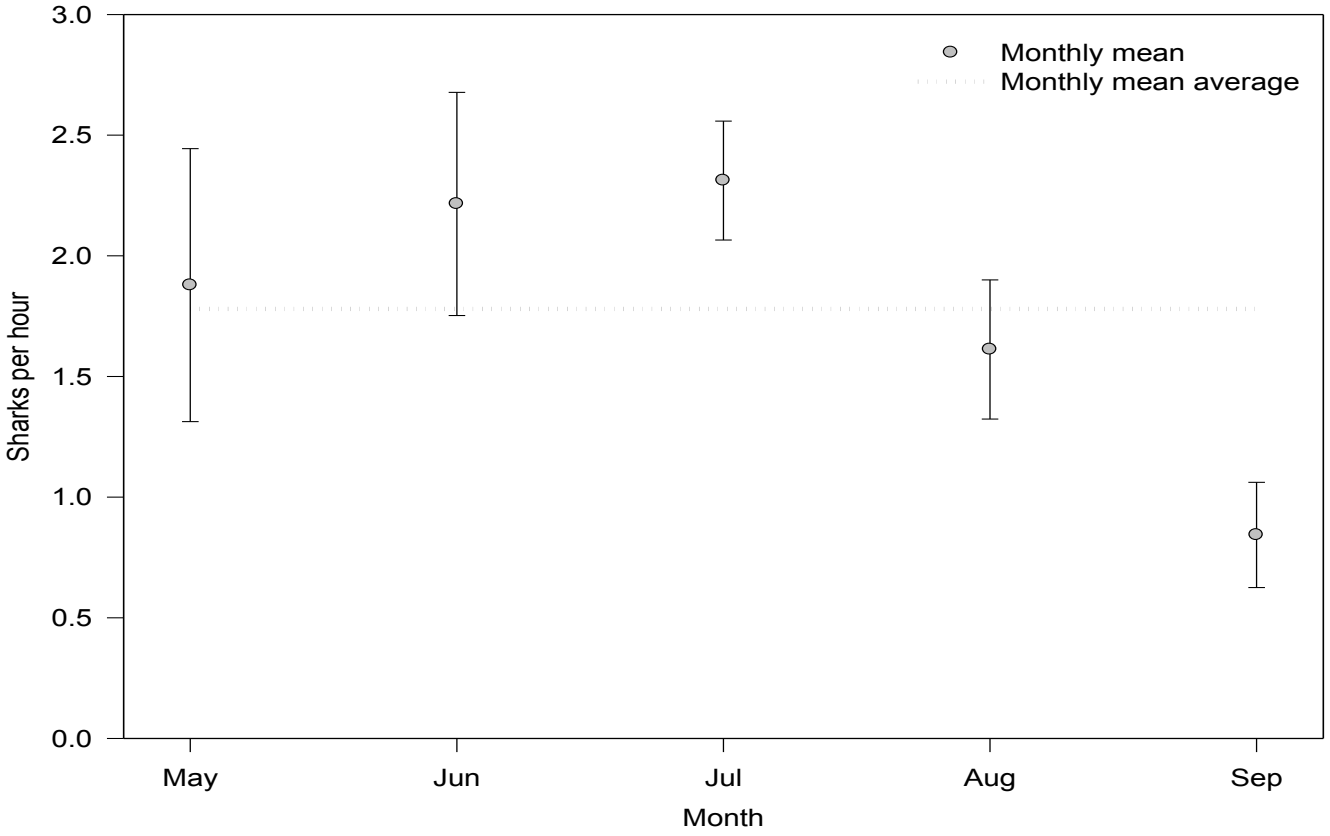

Figure 4.6.Inter-month comparison of mean sighting rates for white sharks at Seal Island. Bars represent mean standard errors.

The MMA_{male}, MMA_{female}, and $MMA_{unsexed}$ shark sighting rates were 0.44 (♂ range 0.11–0.71), 0.54 (♀ range 0.33–0.62), and 0.79 (*U* range 0.40–1.14) sharks per hour, respectively (Table 4.1, Figure 4.7). Male sighting rates in May and August were similar to each other and reflected the MMA_{male} rate. Male sighting rates peaked abruptly in June, but then decreased consistently with each consecutive month over the duration of the aggregation to a minimum in September (Figure 4.7). Female sighting rates were highest and identical in May and August, and were similar, albeit marginally lower, in both June and July (when rates were again identical to each other), then decreased considerably by September. Female sighting rates were generally higher than for males, except in June and July, and did not exhibit a defined peak, as did males. Female sighting rates were clustered closely around the MMA_{female} rate in May–August, demonstrating that females were sighted more consistently across peak months of the aggregation than males (Figure 4.7).

Unsexed shark sighting rates were highest in July, lowest in September, and were higher than rates of males and females in all months except August (when ♀ = *U* shark SPUE) (Figure 4.7). Similar to males, the sighting rate of unsexed sharks peaked dramatically, although the magnitude of the difference for unsexed sharks was larger and the peak was in July, as opposed to June. Female sighting rates were noticeably higher than those of males in September, suggesting that male white sharks dispersed from Seal Island earlier than females, typically from mid- to late-winter from as early as July, but most noticeably over August. Sighting rates for male, female and unsexed sharks all declined markedly by September, which supports the theory that, regardless of sex, white sharks dispersed from Seal Island until the following annual aggregation in autumn.

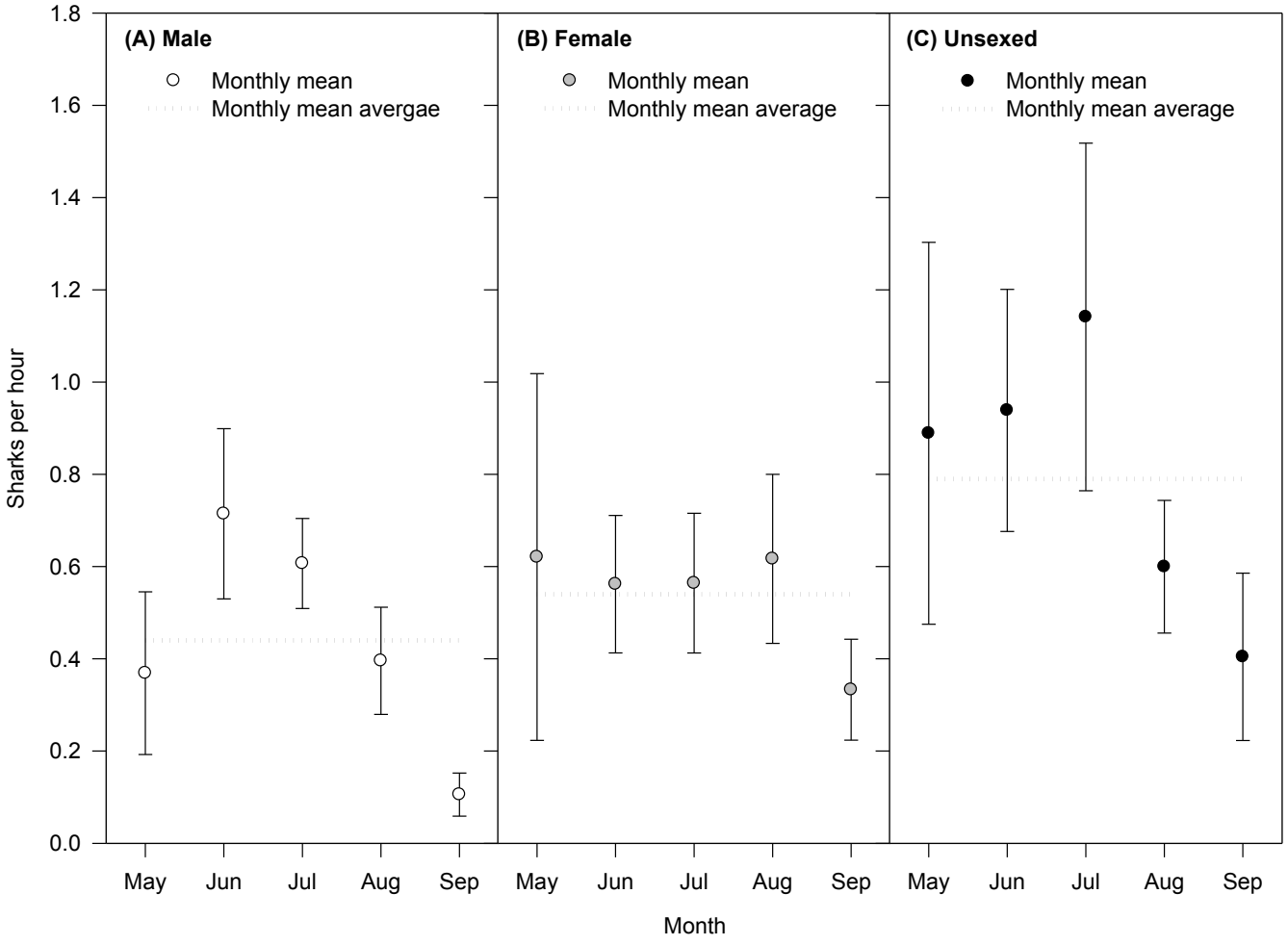

Figure 4.7.Inter-month comparison of mean sighting rates for male, female, and unsexed white sharks at Seal Island. Bars represent mean standard errors.

Temporal variation in sex ratios

Annual trends

The overall AMA_{ratio} was 1.0: 1.0: 2.3 (♂: ♀: *U*) and demonstrates unity of male: female white shark sex ratios at Seal Island, although ratios differed significantly by year and within seasons (Log linear model–$p < 0.001$). Relative to females, males were sighted proportionally more often in four years (2004, 2006, 2010 and 2011) and less often in five years (2005, 2007, 2008, 2009 and 2012), with largest deviations from parity occurring in 2006, 2007 and 2008, and similar ratios in all other years (Table 4.1; Figure 4.8). Unsexed sharks were sighted less often relative to males and females in 2007 and more often in 2006, 2009, 2010, and 2012, when unsexed sharks constituted >50% of sightings (i.e. unsexed shark ratios were greater than the cumulative ratio(s) of both known genders), and ratios departed most disproportionately from the AMA_{ratio}. This suggests recruitment of many sharks, which invariably remained unsexed, into the population in these particular years (supported by significant unsexed shark SPUE rates in 2006 and 2012).

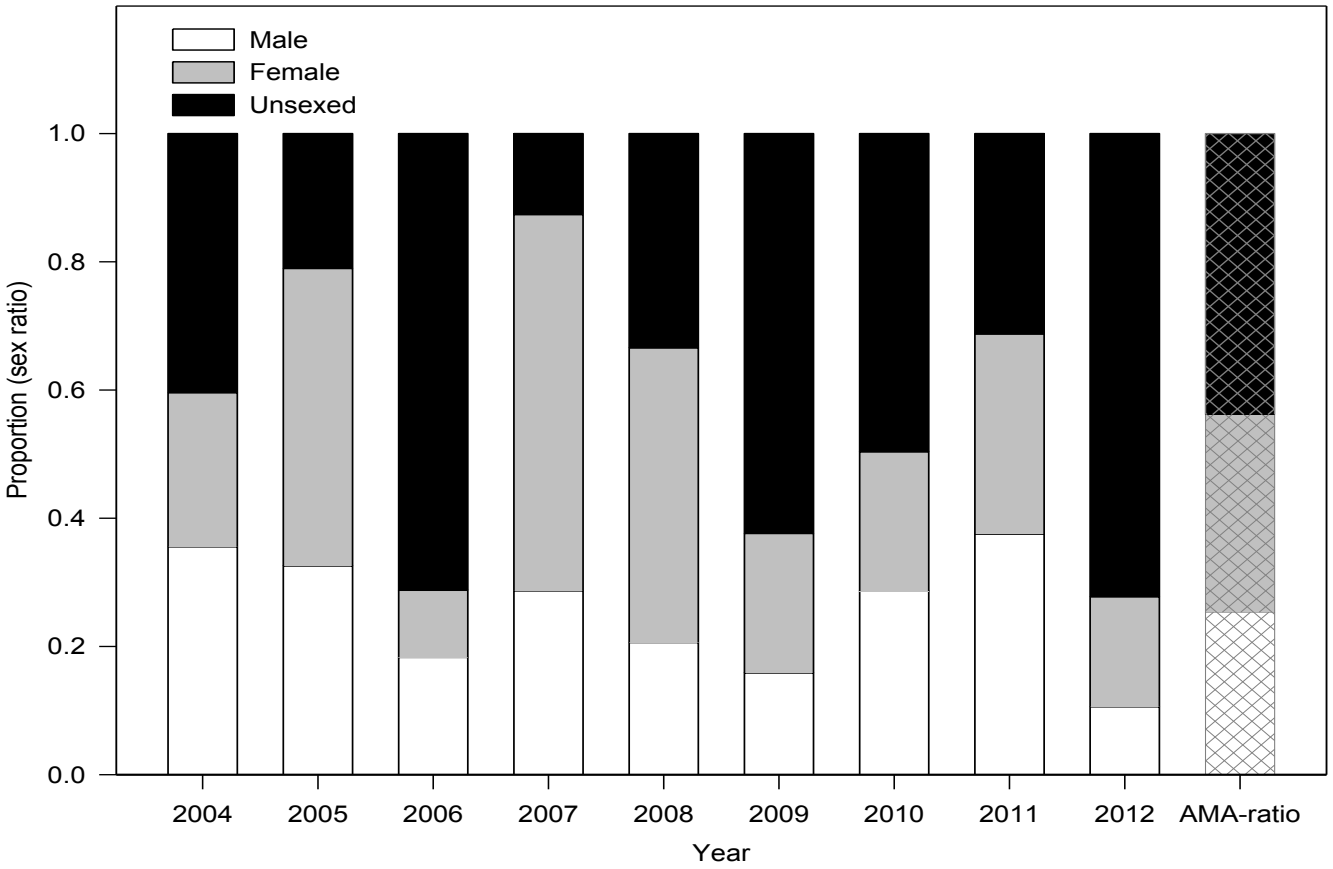

Figure 4.8.Inter-annualsex ratio comparison of white sharks sighted at Seal Island. The annual mean average sex ratios are represented by the grey-hashed column.

Monthly trends

The MMA_{ratio} was 0.8: 1.0: 1.5 (♂: ♀: *U*). Sex ratios varied across all months, but most dramatically in May, August and September, when males were sighted proportionally less often relative to females and unsexed sharks (Table 4.1, Figure 4.9). Males were sighted proportionally most often in June and July, when male and female ratios were closest to parity, and then decreased over August to a minimum in September. Thus, males appear to have resided for one–two months in early to mid-winter, before dispersing in late-winter. In contrast to males, females became proportionally more abundant with each consecutive winter month and peaked in September. Thus, females dominated in autumn and spring months, were sighted more consistently across peak months and did not disperse until spring. At least half of the sharks sighted in May were unsexed, although this group comprised a large and consistent proportion of each other monthly sex ratio and reflected more closely the MMA_{ratio}. Females and unsexed sharks were sighted with equal frequency to each other and proportionally more often than males in September, suggesting that unsexed sharks sighted in later months were probably females, consistent with earlier dispersal of males.

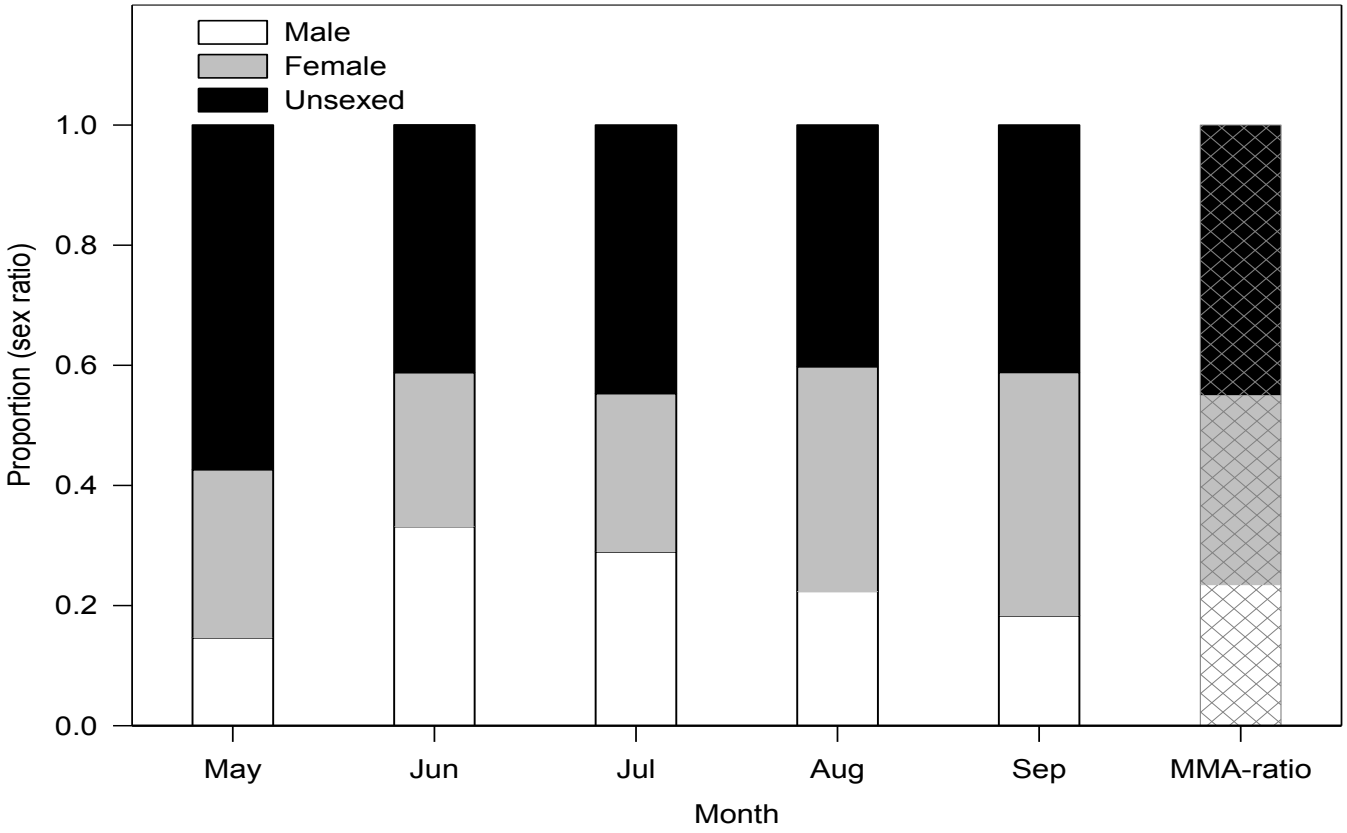

Figure 4.9.Inter-month sex ratio comparison of white sharks sighted at Seal Island. The monthly mean average sex ratios are represented by the grey-hashed column.

Mark-recapture

Occurrence and sightings

Of the total 1105 white shark sightings recorded (2004–2012), 39.2% (n = 433) were photo-identified as new captures (27.4%) and recaptures (11.8%). Of the 433 photographed events, 70% represented 303 captures of different *C. carcharias* (112 ♂, 111 ♀, and 80 *U*), whereas 30% represented 130 recaptures of 88 of the 303 captures. Captures were steadily recruited into the identified population each year (Figure 4.10), but with greatest frequency in 2005, 2006, 2009 and 2010 (when effort and sightings were both highest; see Figure 4.2), and with lowest frequency in 2004, 2007, 2008 and 2012 (when effort and sightings were both lowest; see Figure 4.1), and were particularly low in 2011, considering effort was especially high in that year. Male and female capture frequencies were similar in most years and greater than unsexed sharks in all years. Capture frequencies of unsexed sharks were greatest in 2009. Overall, there was no indication that all white sharks had been identified that visited Seal Island during the nine-year study period, given that the discovery curve (i.e. size of the

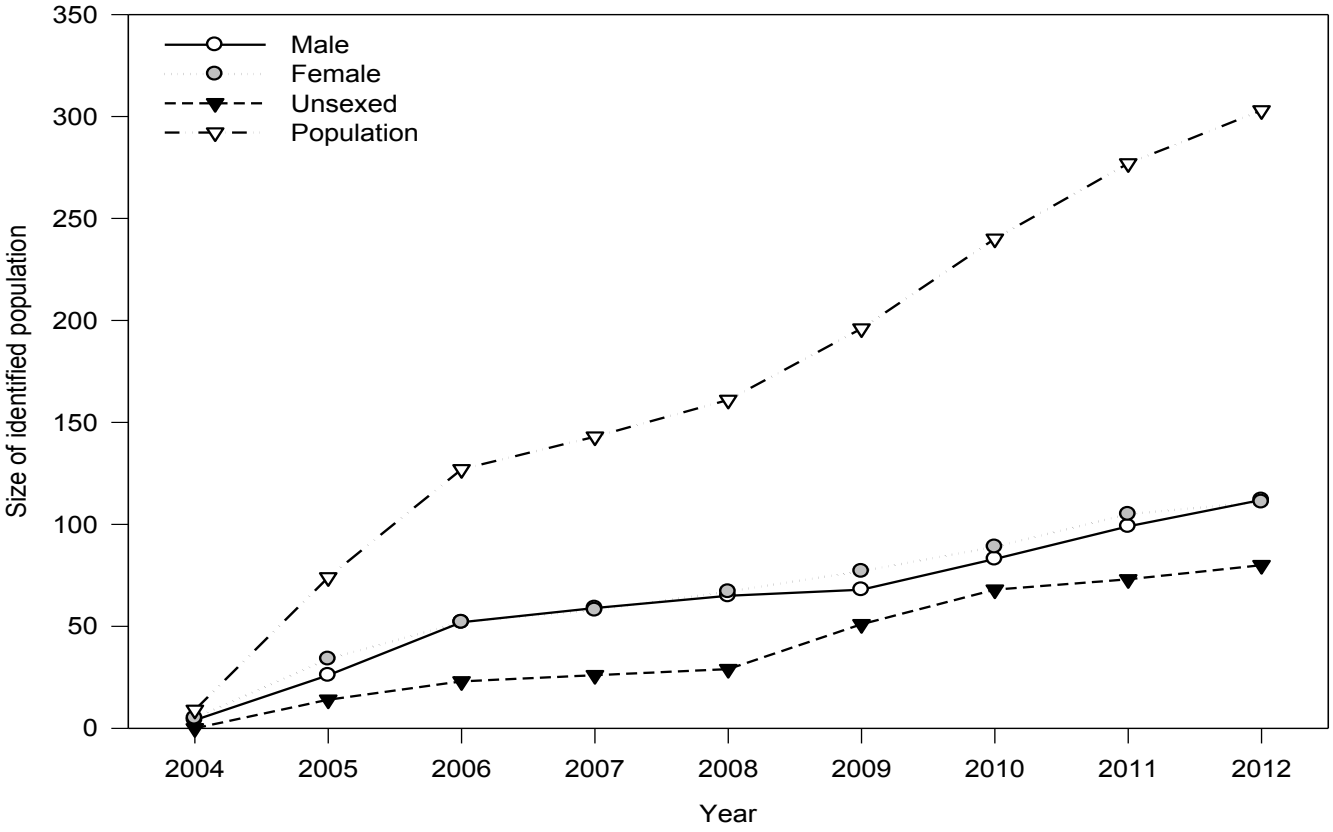

Figure 4.10.Discovery curve illustrating the steady rise in total numbers of newly captured white sharks into the photo-identified population at Seal Island each year.

Photo-ID efficiency

Of the total 1105 sightings recorded, 60.8% went photographically unidentified, while 38.2% were captured (27.4%) and recaptured (11.8%). Mean annual percentages for numbers of identified (captures and recaptures) and unidentified shark sightings were 45% and 55% respectively. In other words, 45% of shark sightings were photographed, whereas 55% were not photographed each year, on average. Therefore, the dorsal fin photo-ID method is only efficient at detecting approximately half of the shark sightings in any year.

Recapture ratios, immigration and emigration

In 2004, 33.3% of the sighted population were identified (n = 9 captures). The ratio of recaptures to new captures, termed interchangeably as the "recapture ratio", was zero in 2004 because this was the first year of the study. In 2005, 27.4% were identified (25.1% captures: 2.3% recaptures). Despite this, captures were highest in 2005 (n = 65) and although recaptures were in fact high in absolute terms (6/9 individuals or 67%), the recapture ratio was skewed low as a result of the disparity i.e. 65: 6 (Figure 4.11). In 2006, 40.0% were identified (25.2% captures: 14.8% recaptures). The recapture ratio increased because 74 sharks, which had been recruited in 2004 and 2005, returned and were readily recaptured with increased effort and consistent sampling. Although many sharks were photo-identified in 2006 overall, sightings were also particularly high. Therefore, many sharks (60%) had in fact evaded photo-identification, suggesting photo-ID efficiency was not optimal, or sharks were over-abundant.

In 2007, 55.8% of sharks were identified (30.8% captures: 25.0% recaptures). The recapture ratio was highest in 2007, demonstrating high recapture frequencies of sharks from previous years and that few new sharks were identified. Although effort, sightings, captures and recaptures, were all low in 2007, the few sharks that were encountered were readily identified and were predominantly females (Figure 4.5). In 2008, 72.5% were identified (45.0% captures: 27.5% recaptures). The recapture ratios in 2008 and 2006 were similar and lower than in 2007. Female sighting rates were particularly high in 2008 (Figure 4.5.), which suggests that more new, but fewer well-known females were present and identified in 2008.

In 2009, 54% were identified (40.7% captures: 14.0% recaptures). The recapture ratio declined markedly with an influx of new sharks in this year (see Figure 4.8: high unsexed sharks sex ratios in 2009), which were successfully captured as a consequence of increased effort and fully saturated photo-ID sampling. Recaptures were particularly low, suggesting

that previously identified sharks had started to emigrate (permanently and/or temporarily) from the population around 2009 and quite possibly as early as 2008, given recaptures were moderate-low by comparison to 2007. It thus seems probable that, with increased effort in 2009, more new sharks were captured during a pulse of immigration, which inflated captures, while the emigration of old sharks deflated recaptures and ultimately skewed the recapture ratio downwards. As effort increased with each consecutive year from 2009–2011 recapture ratios increased sequentially. In 2010, 43.2% were identified (30.1% captures: 13.0% recaptures). The recapture ratio increased with few new recruits captured by comparison to 2009, while recapture percentages were almost identical

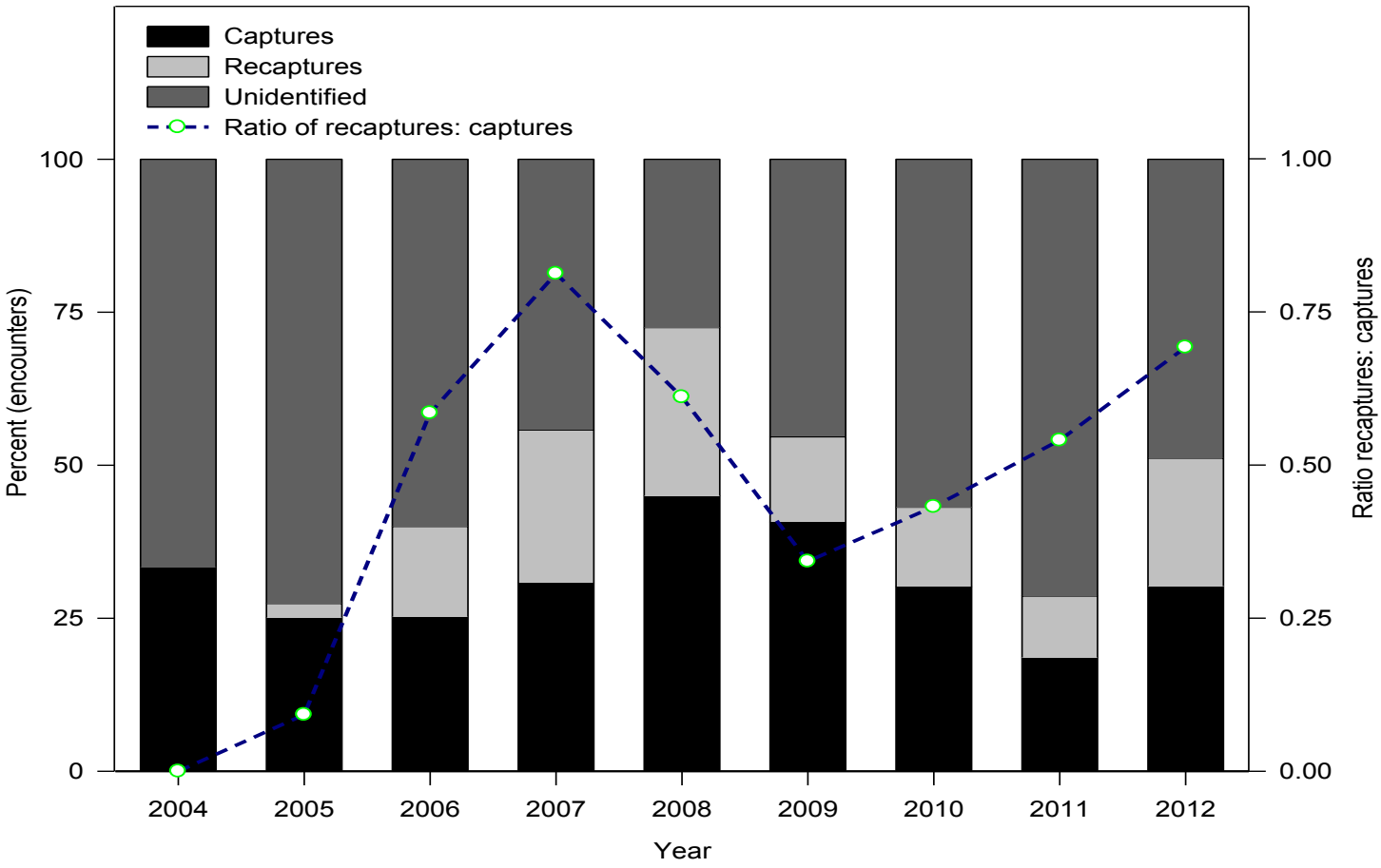

Figure 4.11.Inter-annual comparison of captures, recaptures and photographically unidentified sightings, with ratios of recaptures to new captures of white sharks at Seal Island.

In 2011, 28.6% of sharks were identified (18.6% captures: 10.1% recaptures). The recapture ratio increased further, with even fewer new captures, in 2011 than in 2010, but with similar, albeit slightly lower, numbers of recaptures. Although effort increased and sampling was proficient in these years, fewer new sharks were captured, or known sharks recaptured. In 2012, 51.2% were identified (30.2% captures: 20.9% recaptures). Both

captures and recaptures were moderate-high, which is consistent with field observations in that several well-known mature male sharks were recaptured in 2012 (see Appendix Table A.1, WS0001 and WS0006), as well as a noticeable influx of new juvenile males (< 250 cm TL) and one particularly large mature male shark (~500–550 cm TL). This suggests that 2012 was a year of increased occurrence of male white sharks at Seal Island.

Recapture ratios varied across years and fluctuated with increased shark activity, sampling effort and efficiency. Both captures and recaptures declined over the nine-year study period, despite effort increasing, suggesting that fewer sharks were recruited into or returning to the population. Percentages of unidentified sightings were greater than percentage captures and recaptures in all years except 2008 and greater than both percentage captures and recaptures in all years except 2007–2009 (Figure 4.11). It therefore appears that certain white sharks are inherently more difficult to capture than others, and hence, they typically remain unsexed and rarely photographed (60.8% of all sightings were unidentified overall), which is indicative of "trap-shy" behaviour in this group of intractable individuals.

Residents and transients

In total, 49% (n = 149) of the 303 identified sharks remained unmatched in the database. As such, approximately half of the individuals in the monitored population at Seal Island were transient and never recaptured. In contrast, 51% (n = 155) were recaptured during at least one other survey at least 18 h apart. Using the compressed annual capture history structure with nine sampling occasions, i.e. years (see Chapter 3), 71% (n = 215) of all sharks were transients (captured in a single year), whereas 29% (n = 88) were residents (recaptured in at least one other year, but not necessarily the following year).

One hundred and thirty recaptures were photographed for the 88 resident white sharks (40% ♂, 45% ♀, and 15% *U*), 70% of which were recaptured in a single other year (27% ♂, 30% ♀, 13% *U*), 19% in two other years (7% ♂, 10% ♀, 2% *U*), 10% in three other years (5% ♂, 5% ♀), a single female in four years (1%) and one male "WS0001" in six (1%) out of eight possible years. Eighty-six percent of unsexed sharks were recaptured in a single year and all were recaptured in no more than two years, supporting high rates of transience and/or "trap shy" behaviour. There was no significant departure from unity in recapture frequencies by sex ($\chi^2 = 21.00$, $df = 22$, $p = 0.52$) (Figure 4.12).

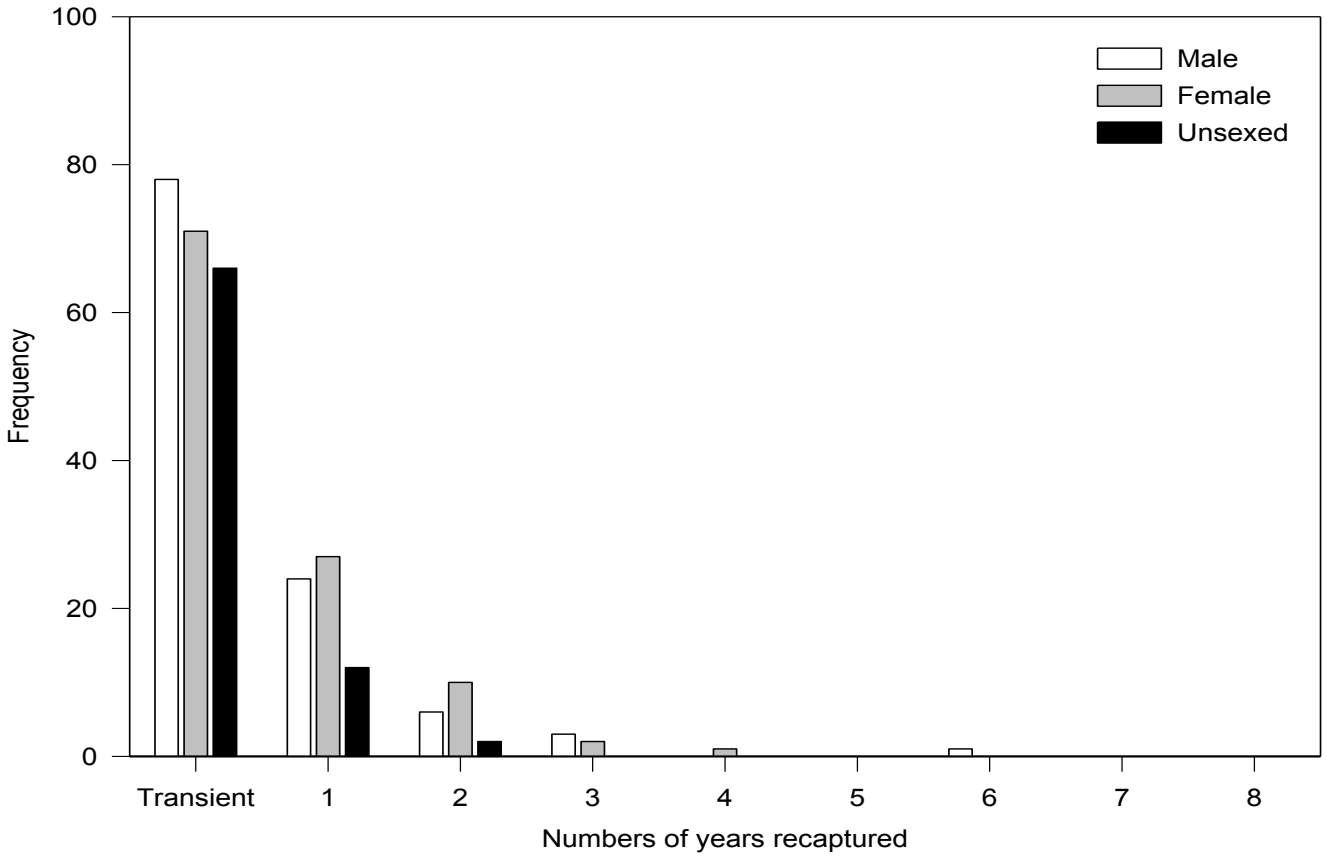

Figure 4.12.Summarised annual numbers of recaptures by sex of white sharks at Seal Island.

The vast majority (98%) of resident sharks were recaptured in > 3 y, with 35% skipping one or more years between recaptures, indicative of temporary emigration, with no differences between male (14.0%) and female sharks (14.0%). The other 65% of residents (24% ♂, 30.8% ♀, and 10.3% *U*) were recaptured the following year and/or subsequent years, indicative of short term site fidelity to Seal Island over 2-3 y periods. Female sharks were recaptured marginally (6.8%) more often than males the following year after capture and demonstrated stronger residency than males over short time-periods. However, after 2–3 y visitation bouts, large females approaching size-at-maturity (> 450 cm TL), consistently dispersed and were rarely recaptured. Limited evidence suggested that certain males returned annually and might demonstrate long-term fidelity to Seal Island, particularly as adults (see Appendix Table A.1, WS0001* and WS0006).

Size distribution

Of the total 433 encounters photographed, 366 had size-related data (44% ♂, 46% ♀: 10%*U*). Mean total lengths (TL) were estimated at 315 (± 3.9 SE, ♂), 330 (± 4.2 SE, ♀) and 322 cm (± 8.2 SE, *U*). In total, 1% were sized 150–199 cm(YOY), 6% 200–249 cm, 21% 250–299 cm, 54% 300–349 cm, 10% 350–399 cm, 7% 400–449 cm, with large sharks (450–549 cm) comprising 1.6% (Figure 4.13). Only three sharks (1%) > 500 cm (1 ♂: 1 ♀: 1 *U*) and no sharks > 550 cm were encountered. Overall, 72% of sharks were sized > 300 cm. There was no significant departure from unity in size frequencies by sex ($\chi^2 = 16.92$, $df = 14$, $p = 0.26$).

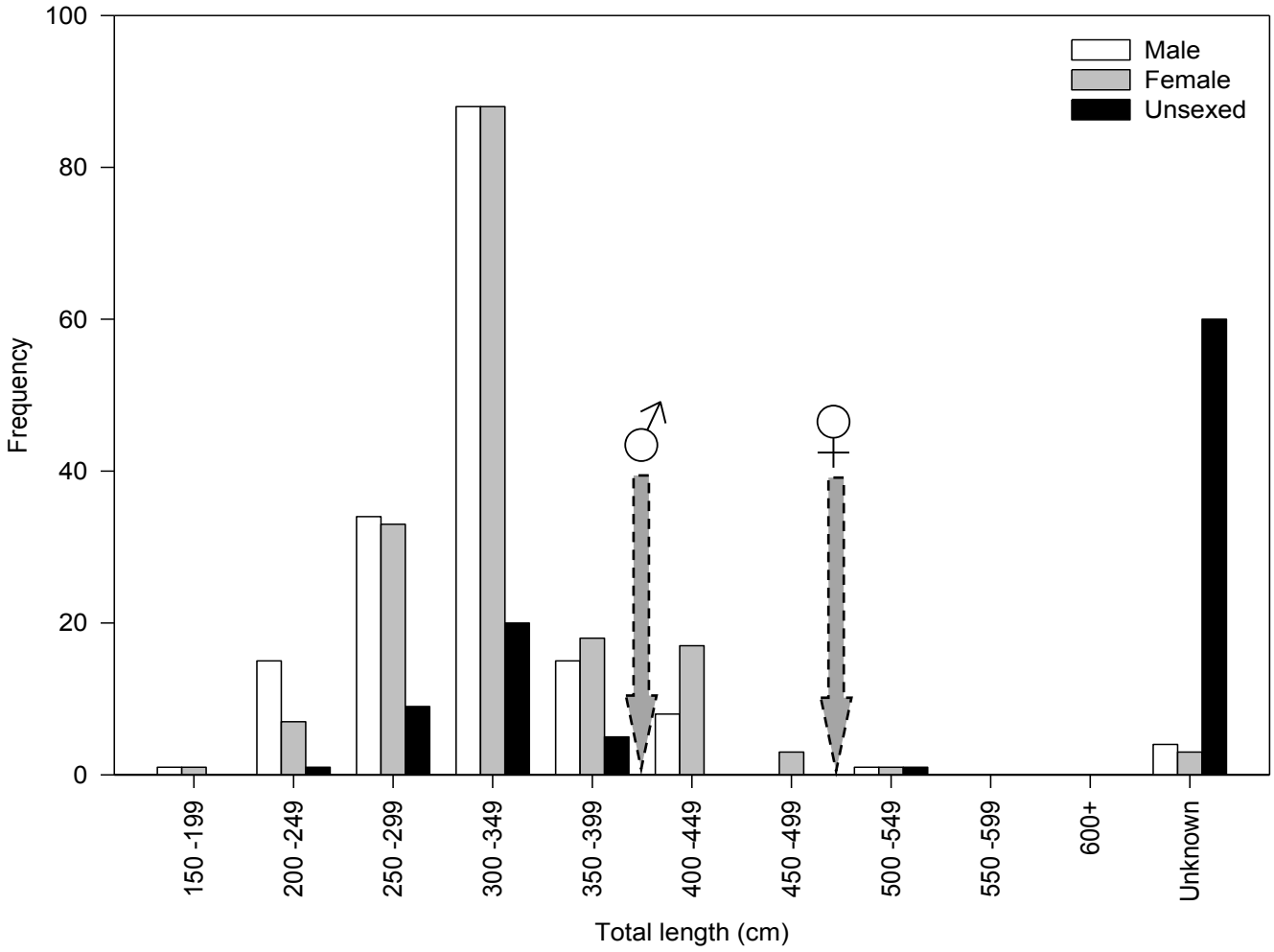

Figure 4.13.Total length size distribution for photo-identified white sharks at Seal Island. Arrows represent minimum size-at-maturity for males (♂) and females (♀).

Maturity composition

In total, 330 encounters with male and female white sharks had size-related data. Of these, 60% were classed as immature (0.3: 1.0, ♂: ♀), 32% as subadult (5.2: 1.0, ♂: ♀), and 8% as mature (6.0: 1.0, ♂: ♀) (Figure 4.14). A respective 1, 27, and 7% of male sharks were immature, subadult and mature, whereas 45 and 5% of females were immature and subadult, respectively, and 1% were mature, using 450 cm as the lower boundary of female size-at-maturity. Maturity stage of male and female sharks departed significantly from unity (χ^2 = 109.98, $df = 2$, $p < 0.001$). Ratios of subadult and mature males were significantly higher than female ratios in the same maturity class. At least 40% of the identified population at Seal Island were subadult and mature white sharks, particularly males (34%) and large females (6%).

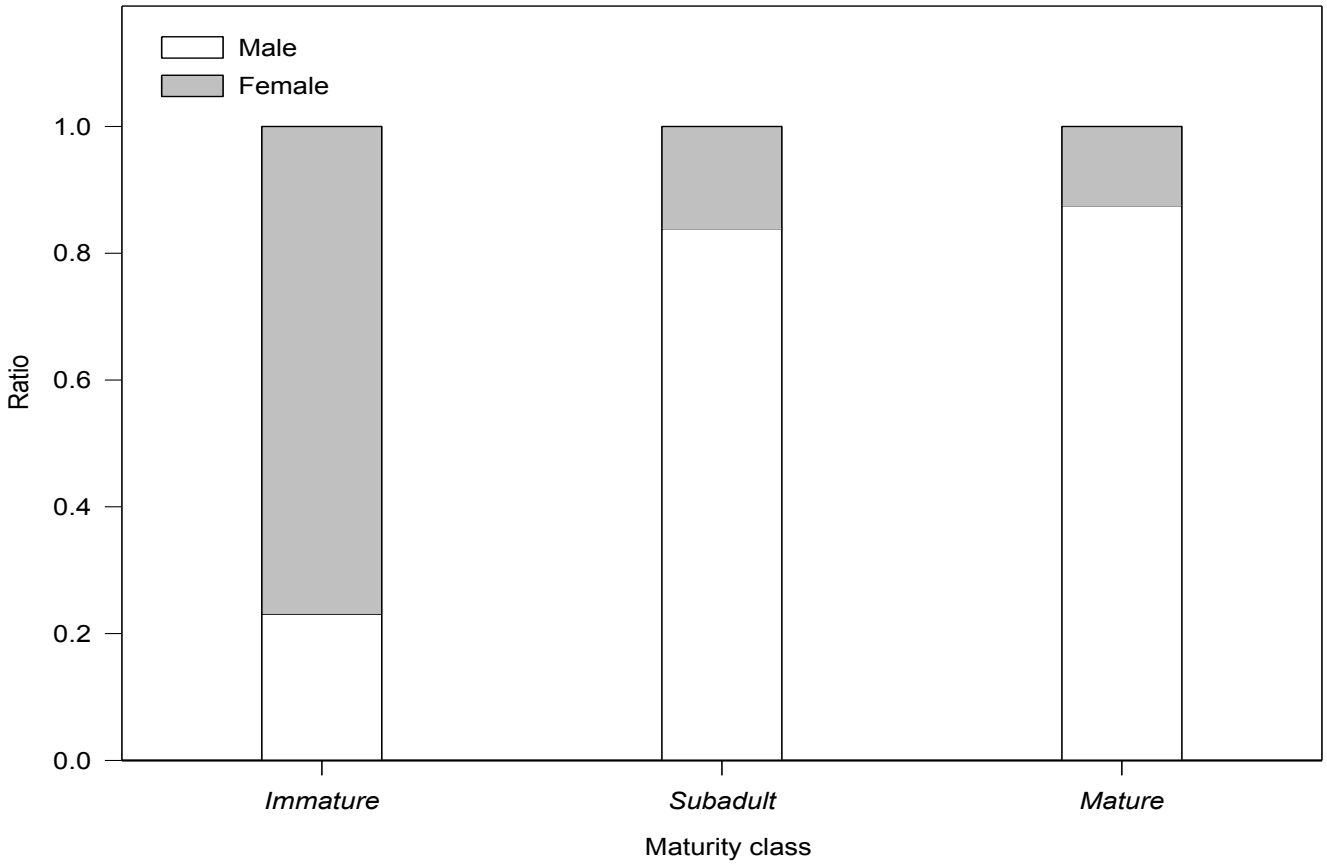

Figure 4.14.Maturity comparison for ratios of identified white sharks at Seal Island.

DISCUSSION

Migratory predators can increase their probability of encountering prey by targeting specific habitats and selecting optimum times to visit these sites, when prey are most accessible to them (Heithaus, 2004; Hammerschlag *et al*., 2006). Thus, if a predator aggregation forms on the basis of foraging, one would expect that peaks in predatory activity would be correlated with periods when biotic and abiotic factors are optimal for prey exploitation (Rogers *et al*., 1984; Sundström *et al*., 2001; Heithaus, 2004; Hammerschlag *et al*., 2006).

The white shark aggregation at Seal Island exhibits a highly distinct seasonal visitation pattern between May and September (range February–October). The earliest arrivals of sharks and active predations on Cape fur seals coincide with increased availability of naive seal pups in autumn months (Laroche *et al*., 2008; Kock *et al*., 2013). Hammerschlag *et al*. (2006) reported peaks in predatory activity of sharks between May and August, which supports the findings of this study in that sighting rates were highest over this exact period. Multiple studies have demonstrated that white sharks are seasonally abundant around seal colonies in winter months in South Africa (Cliff *et al*., 1996a; Ferreira and Ferreira, 1996; Jewell *et al*., 2011; Kock *et al*., 2013; Towner *et al*., 2013), summer in both South Australia (Bruce, 1992; Robbins and Booth, 2012) and off the US East Coast (Casey and Pratt, 1985; Skomal *et al*., 2012), and autumn off the US West Coast, off Central California (Ainley *et al*., 1981; Klimley, 1985; Klimley *et al*., 1992) and at Guadeloupe Island (Nasby-Lucas and Domeier, 2012). Trends in occurrence of large white sharks have been directly linked to increased seasonal availability of pinnipeds in South Africa (Martin *et al*., 2005; Kock and Johnson, 2006; Kock *et al*., 2013), California (Ainley *et al*., 1985) and South Australia (Robbins and Booth, 2012; Semmens *et al*., 2013), suggesting that energetically valuable prey availability is one factor influencing the distribution of large white sharks, worldwide.

Despite such a strong seasonal trend in shark occurrence at Seal Island, sighting rates were highly variable across years and decreased over the nine-year study period, significantly between 2006 and both 2009 and 2011. In later years, sharks were generally less abundant, sighted more infrequently, and revisited the aggregation site less over time. Therefore, while prey availability might be one factor that dictates white shark distribution, it is possible that other variables, such as sea-surface-temperature (SST) (Cliff *et al*., 1996a; Towner *et al*., 2013; Weltz *et al*., 2013), barometric pressure (Dicken *et al*., 2013), or behaviour of sharks

related to reproduction or other important aspects of *C. carcharias* life history, might have influenced inter-annual trends in sighting rates and the population composition at Seal Island.

It is possible that large-scale meteorological phenomenon might be underlying inter-annual trends in shark sighting rates at Seal Island. Cliff *et al*. (1996a) reported marked cyclical peaks in catches of white sharks in the nets along the KwaZulu-Natal (KZN) coast every 4–6 y (1968, 1973, 1978, 1984 and 1989). Annual sighting rates at Seal Island were assessed by extending the 4–6 y cyclical peaks through time at four, five and six year intervals, assuming the trend was a shared feature of the white shark population in South Africa. Hypothesised peak years at four year intervals were 1993, 1997, 2001, 2005, 2009 and 2012; at five year intervals 1994, 1999, 2004, 2009 and 2013; and at six year intervals 1995, 2001, 2007 and 2012. It is evident from this range of years that 2004, 2005, 2007, and both 2009, and 2012, were common or shared years for prospective increases in white shark abundance along the coast.

Cliff (Pers. comm. 2013, citing KZNSB unpublished catch rate data) confirmed a peak in catches of white sharks in the nets in 2005, although these data still require robust analysis. Sighting rates at Seal Island were highest in 2005 and 2006, which is highly consistent with prospective peaks at four-year intervals and the confirmed increase in catches in 2005 in KZN (Cliff, 2013 Pers. comm.). Sighting rates decreased in 2007 and 2008 and further still in 2009–2011, with sharks noticeably scarce by comparison to previous years. The sighting rate in 2012 was greater than in 2009–2011, and identical to the $AMA_{population}$ rate of the study. Thus, 2005–2006, and 2012–2013, might reflect peak years consistent with six-year intervals, although effort was low in 2012, and estimates should therefore be interpreted cautiously.

Male sighting rates peaked in 2005, consistent with a hypothesised peak year, and again five years later in 2010. Female sighting rates peaked in 2005, 2007 and 2008, and were clustered around this early-mid period in the study, and did not peak in later years. This suggests that a large number of female sharks had dispersed from 2009 onwards. Unsexed shark sighting rates in 2006 were significantly higher than sighting rates of male, female and unsexed sharks, in all years, except unsexed sharks in 2012. This suggests that 2006 and 2012 (separated by a six year interval), were years of increased recruitment of new sharks to the study, but not necessarily YOY or juveniles. It therefore appears that the 4–6 year cyclical peaks described by Cliff *et al*., (1996a) might partially explain inter-annual trends in white shark sighting rates at Seal Island.

Cliff *et al*., (1996a) concluded that increased winter catch rates were correlated with high rainfall and a low SST during the preceding summer in the cold phase of ENSO, La Nina (Schumann *et al*., 1996). In KZN, meteorological and oceanographic signals include increased easterly wind flow, water turbidity and coastal upwelling (Cliff *et al*., 1996a). Increased easterly winds enhance SST gradients on the landward edge of the warm Agulhas Current, which reduces SST during upwelling. As a result, white sharks appear to move inshore into cooler water in to the vicinity of the nets, with 63% of catches between 19 and 21°C (range = 17–26°C), thus increasing catch rates in winter months (Cliff *et al*., 1996a). Other studies have reported increased occurrence of white sharks during periods of upwelling in Gansbaai, South Africa (Towner *et al*., 2013), California (Pyle *et al*., 1996) and off the Brazilian coast (Gadig and Rosa, 1996).

Catches of white sharks in the KZN nets were reported throughout the year, but were highest in the second half of each year, particularly in winter months (i.e. peaks in July in 1978–1988 and August in 1989–1993 in Cliff *et al*., 1989, 1996a). Interestingly, this trend in highest catches coincides with peak months in sighting rates at Seal Island. Male sighting rates peaked in June, but consistently decreased with each month thereafter as males dispersed from July onwards. Males were rarely sighted in September, which suggests complete dispersal of males by spring. Kock *et al*. (2013) hypothesised that male sharks leave False Bay, and hence Seal Island, over spring and summer months, consistent with the findings of this study. In contrast to males, female sighting rates were higher in both August and September. This suggests that females remained at Seal Island until later months of the aggregation, which ceased each year in September, as sharks, irrespective of sex, dispersed away from the seal colony. This suggests that females resided for longer within each season than males, which is consistent with females remaining in the Bay before dispersing from the island and colonising inshore areas in spring months (Kock *et al*., 2013). Female white sharks are, however, unlikely to be restricted to False Bay during sexual segregation. Given that catches in KZN were highest in the latter half of each year, it seems highly probable that the nets catch white sharks that have migrated east after having preyed upon Cape fur seals around their colonies in the Western Cape in autumn-winter. This is supported from stomach content analyses of large white sharks caught in KZN, in which *A. pusillus* and other marine mammal remains were predominant (Cliff *et al*., 1989; Hussey *et al*., 2012). It is probable that white sharks are foraging on prey resources at sites within Mozambique, which suggests that Mozambique and other eastern regions of Africa might form important habitat.

Sex ratios

White sharks are known to segregate by sex seasonally in the north-eastern Pacific (Domeier and Nasby-Lucas, 2012), off the US West (Klimley, 1985) and East Coasts (Pratt, 1979), off Australia‟s South Coast (Strong *et al*., 1996; Robbins and Booth, 2012), and in South Africa in False Bay (Kock *et al*., 2013). Despite female white sharks segregating seasonally by sex inshore in spring and summer months in False Bay (Kock *et al*., 2013), sexual segregation was not evident at Seal Island in the current study. Cliff *et al*. (1989) reported ~50% more female white sharks (n = 591) caught in the nets off KZN. Given the geographical extent of the netted region, its continuous fishing effort over the last five decades, and the sample size, general span and accuracy of the data set assessed, it is possible that this female dominated ratio is reflective of the true population sex ratio in South Africa. However, this is unlikely given that no mature female white sharks and only three mature males have been caught in the nets since 1952 (Dudley, 2012), and the mean total length for sharks in KZN was smaller than those of white sharks at Western Cape sites (250 and 320 cm TL, respectively). This suggests that a subcomponent of the population was sampled in KZN, i.e. predominantly juveniles to the exclusion of mature sharks. Given these biases, ratio data from the nets could also potentially be skewed. Furthermore, the KZN coastline has no associated seal colonies and comprises habitat similar to coastal sites in the Western Cape, like northern shore areas of False Bay, or Struisbaai, for example. As such, the nets fish year-round close inshore in coastal habitat. Although sexual segregation inshore in spring and summer in KZN has not been assessed, it is possible that during segregation females might be exposed to higher incidental catches in the nets, which could account for the slight female-biased ratio reported by Cliff *et al*. (1989). Areas off Richard‟s Bay and other sites off the KZN coast appear to be important habitat for male white sharks, which remain semi-residential in the area for extended periods, i.e. 2–3 months, and also regularly move through the netted region using what appears to be a migratory corridor to Mozambique (Ocearch Shark Tracker, unpublished data). As such, males are still captured with relatively high frequency in the nets, which could account for why the ratio is not highly skewed towards females.

However, other studies have also reported female biased sex ratios in South Africa. Ryklief (2012) reported strongly female biased sex ratios at Mossel Bay. However, white sharks were typically juveniles (e.g. 85% sized 150–340 cm TL), which can make accurate sexing of sharks difficult, because claspers are typically under-developed and are therefore not easily observed. Furthermore, a large proportion of sampling took place at three inshore

sites during segregation, when females are conspicuous inshore and when males tend to be rarely encountered (Johnson, 2003; Kock *et al*., 2013; Pers. Obs). Ryklief's (2012) findings for Mossel Bay are consistent with Ferreira and Ferreira's (1996) observations and extreme female bias at Dyer Island and at Struisbaai. However, similar to Mossel Bay, the majority of sampling took place in spring and summer months at Dyer Island and Struisbaai (an inshore site), which again suggests that males were under-sampled and females were over-sampled during sexual segregation, which therefore skewed the ratio towards females. Similarly, Dicken *et al*. (2013) reported a female-biased sex ratio at Bird Island. It does seem, however, that female white sharks are either generally more abundant than males, or perhaps females are detectable more often than males i.e. once males have dispersed, females then segregate inshore over spring and summer months when sampling also occurs with high intensity at sites in Gansbaai, Struisbaai, Mossel Bay and KZN. Therefore, the equal sex ratio reported for large white sharks at Seal Island, i.e. 72.6% > 300 cm TL, suggests that the sexual composition of subadult and adult *C. carcharias* in South Africa is even closer to unity than ratios reported for all other sites, where juveniles have predominantly been sampled and seasonal sampling biases have been incurred (Cliff *et al*., 1989, Ferreira and Ferreira, 1996; Ryklief, 2012; Dicken *et al*., 2013).

Strong *et al*. (1996) reported that sexes were spatio-temporally segregated in South Australia, with females dominant at Dangerous Reef and other inshore sites in winter months, whereas males predominated at the Neptune Islands and other offshore sites in summer months. Despite spatial and temporal sex segregation, Strong *et al*. (1996) reported an equal sex ratio for the population in South Australia (1.0: 1.0, ♂: ♀), which is identical to the sex ratio at Seal Island. Strong *et al*. (1996) noted that winter was the only period when mixing of male and female sharks occurred at Dangerous Reef, which perhaps corresponded with the mating season in this region. However, despite a similar period of overlap of sexes in winter at Seal Island, no direct observations of mating behaviour were recorded. Although bite marks were observed on females on occasion, that were consistent with copulation, bites were generally not fresh and were also observed on males and small sharks (< 250 cm TL), suggesting that intra-specific aggression may account for a proportion of these observations. It therefore seems unlikely that white sharks are mating during the aggregation at Seal Island, although this cannot be completely discounted.

More recently, at the Neptune Islands, Robbins and Booth (2012) reported a male-biased sex ratio. Mature females were only encountered in autumn and winter, when SST's

were warmer, whereas males were prevalent in summer months when SST‟s were cooler. Cold water temperatures have been hypothesised to assist in sperm production in other male elasmobranchs, such as dogfish (Kime and Hews, 1982), whereas behavioural shifts of mature females into warmer water might increase reproductive output by hastening physiological development of females and embryos, as has been suggested for other mature female elasmobranchs that segregate in warmer waters (Klimley, 1985b). Inter-annual variation was evident at Seal Island with ratios of male sharks higher than females in 2004, 2006, 2010 and 2011, but lower than females in 2005, 2007, 2008, 2009 and 2012, which might have been related to water temperature fluctuations, and provides an important avenue for future research.

In contrast to Seal Island, but similar to the Neptune Islands, Nasby-Lucas and Domeier (2012) reported a male biased sex ratio at Guadeloupe Island. The sex ratio reached equality in November, although effort past December was minimal and may have skewed the ratio (Nasby-Lucas and Domeier, 2012). However, male dominated ratios have also been reported for white sharks off Central California (Chapple *et al*., 2011) and off New Caledonia in the South Pacific (Clua and Seret, 2012). Domeier (2012) noted that while mature females were inshore, they quite probably mated at sites like Guadeloupe Island, as the period of overlap between sexes was short (90–120 days over a two year period), before complete segregation occurred again within offshore habitat (Domeier and Nasby-Lucas, 2012). This 90–120 day period of overlap was similar at Seal Island (May–August), with both sexes abundant in winter months, and males dispersing completely by spring before females segregated inshore (Kock *et al*., 2013).

Mark-recapture: Occurrence and sightings

Despite nine years of photo-ID sampling, the entire population was not identified; 61% of all sightings remained photographically unidentified. Capture frequencies of male and female sharks were similar in most years and were greater than for unsexed sharks in all years. This suggests that certain sharks behave more intractably than others and are therefore more difficult to capture. This is indicative of “trap-shy” behaviour (see Chapter 5) and is supported by almost ubiquitous decreasing response times of sharks to baiting activities at this site (Laroche *et al*. (2007).

Frequencies of captures were greater than recaptures in all years, and although new sharks were identified annually, sightings, captures and recaptures all decreased in later

years, suggesting that fewer sharks recruited into, or returned to, the population. This was surprising, given such high effort and persistent sampling in mid-later years (2009–2012), and particularly in 2011, when sampling effort was high, but captures were especially low. In contrast, sharks were abundant, but effort was lowest and most variable, in early-mid years (2004–2008). Although effort was moderate in 2009 compared to 2011, large numbers of „new" unsexed sharks immigrated into the population and were effectively captured in 2009 (see Chapter 5); a hypothesised peak year (Cliff *et al*., 1996a). Recaptures showed that most large white sharks encountered in 2004–2007 dispersed from the population between 2008 and 2009 and were rarely recaptured in later years (see Appendix Table A.1). Presumably the sharks that dispersed in this period were now mature, given that five to nine years had passed, and most sharks were already approaching maturity and were some of largest white sharks encountered anywhere in South Africa at that time (Kock and Johnson, 2006). What is more, effort and sampling efficiency increased dramatically in later years, suggesting it is unlikely that these large adult sharks would have been missed and further supports the notion that mature female white sharks permanently or have temporarily emigrated from the population.

Approximately half of the 303 identified white sharks at Seal Island remained unmatched in the database. Considering recaptures across years, 71% were transient, whereas 29% were resident. In stark contrast, Nasby-Lucas and Domeier (2012) reported extreme seasonal site fidelity of white sharks to Guadeloupe Island, with zero transients in the population and all study subjects recaptured during their nine-year study (e.g. 82% resighted in two years and 28% in five years). Females demonstrated a non-consecutive year visitation-pattern (Nasby-Lucas and Domeier, 2012), with a small percentage of mature females exhibiting a consistent every-other-year pattern, indicative of temporary emigration, which was hypothesised to be associated with an 18-month gestation cycle (Domeier, 2012). At Seal Island, approximately 35% of resident sharks temporarily emigrated, skipping one or more years between capture and recapture, with no differences between male and female sharks, and little similarity to the behaviour of sharks in Mexico.

The vast majority (98%) of resident sharks were recaptured in < 3 y, indicating high rates of emigration from the population after short-term bouts of fidelity to Seal Island. Approximately 65% of residents were recaptured the following year(s), suggesting short-term fidelity to this site (~2–3 y), with female sharks demonstrating the trend more strongly than males overall. While mature females exhibited a biannual visitation-pattern at Guadeloupe Island, with strong fidelity over long time-periods, large females demonstrated strong fidelity

to Seal Island over short time-periods (2–3 consecutive years), followed by permanent emigration as they approached 450 cm TL.

At Guadeloupe Island, mature males were consistently encountered in consecutive years (Nasby-Lucas and Domeier, 2012). Anderson *et al*. (2011) also reported long-term fidelity of five male white sharks to Central Californian sites, over periods of between 16 and 22 years, although no shark was detected every year and effort was reportedly variable. Limited evidence demonstrated that certain male sharks exhibited fidelity to Seal Island over long time-periods, possibly visiting every year, and particularly as adults (see Appendix Table A.1, WS0001* and WS0006). Although mature male sharks at both Seal Island and Guadeloupe Island appear to demonstrate long-term annual site-fidelity, the visitation pattern was more marked and highly consistent for mature males off Mexico.

Although large subadult and mature white sharks are observed at both Seal Island and Guadeloupe Island, white sharks appear to behave markedly different at these two aggregation sites, particularly females. As such, the major driving factors responsible for their occurrence at these sites presumably differ. Guadeloupe Island has been proposed as a mating area (Domeier, 2012), whereas Seal Island is perhaps more appropriately characterised as a foraging ground for maturing white sharks. Given that the aggregation in Mexico is primarily thought to form in response to mating (Domeier, 2012), it is probable that white sharks demonstrate greater fidelity to capitalise on mating encounters. In contrast, given that white sharks are presumed to aggregate at Seal Island in response to seasonal prey availability (Kock *et al*., 2013), it is possible that as prey distribution shifts, both spatially and temporally, and as prey becomes more or less abundant at other sites, white sharks shift their movements in response (Bass, 1978; Ferreira and Ferreira, 1996). As a consequence, sharks might exhibit lower fidelity to Seal Island. However, whilst this accounts for temporary emigration of sharks even over relatively long periods of absence, i.e. 3–4 years, it does not explain high rates of permanent emigration, especially when Seal Island is considered to be such an important foraging ground for large sharks. This suggests that other factors are influencing movement patterns of white sharks at, or perhaps more appropriately, from, Seal Island.

Size distribution and maturity composition

The size range of white sharks at Seal Island was 150–549 cm TL, with sharks sized 300–349 cm TL most frequently photographed (53.6%). Size segregation was not evident for male and

female sharks, which were identified in all size classes up to 549 cm TL (except for male sharks sized ~450–499 cm TL, but included one huge male estimated at 500–549 cm TL in 2012). White sharks observed in Gansbaai and Struisbaai ranged in size from 150–500 cm TL (Ferreira and Ferreira, 1996), whereas sharks at Mossel Bay, Bird Island, and off the KZN coast, ranged from 150–450 cm TL (Wallet, 1978; Cliff *et al*., 1989; Ryklief, 2012; Dicken *et al*., 2013). This supports longitudinal distribution of size classes similar to shark populations off the US coasts (Casey and Pratt, 1985; Klimley, 1985; Domeier, 2012). The total length size range for white sharks off Central California was 260–530 cm TL (Chapple *et al*., 2011). Similarly, Strong *et al*. (1996) reported that white sharks from the Spencer Gulf region of South Australia ranged in size from~220–550 cm TL. Sexes were spatially and temporally distributed, but they were not segregated by size (Strong *et al*., 1996), and their distribution did not resemble the longitudinal structure of the South African and US stocks.

Mean total length for the identified population at Seal Island was 322 cm TL (±2.7 SE), which is similar to the 320 cm TL mean reported for white sharks in Gansbaai and Struisbaai (Ferreira and Ferreira, 1996), but considerably larger than the mean length of 250 cm TL in KZN (Wallet, 1973; Cliff *et al*., 1989). Mean total lengths for photo-identified male (315 cm ±3.9 SE) and female (330 cm ±4.2 SE) sharks at Seal Island were similar to those reported by Ferreira and Ferreira (1996), although males were considerably smaller at Struisbaai than at Dyer Island. White sharks are known to move between these three main aggregation sites in the Western Cape (Kock and Johnson, 2006; Ocearch Shark Tracker, unpublished data), which might account for a similar mean size of females. Although these sites host similar mean sized female sharks, subadult and mature males seem to be predominant at Dyer Island and particularly at Seal Island in winter months. Given that certain mature males seem to return to these sites almost every year (Appendix Figure A1, WS0001), this suggests that these two seal colonies in the Western Cape are particularly important habitats for mature male white sharks in South Africa. Mean total lengths reported for Western Cape sites were similar, albeit marginally smaller, than the mean ~370 cm TL reported for males and females in South Australia (Strong *et al*., 1996). Although mean total lengths were similar the size distributions of sharks were different between these two geographically distinct populations.

Young-of-the-year sharks (~150–199 cm TL), constituted 1% of the photo-identified population at Seal Island, with 7% reported in this size class in Gansbaai and Struisbaai (Ferreira and Ferreira, 1996), and 4% in Mossel Bay (Ryklief, 2012) and at Bird Island

(Dicken *et al*., 2013). Catches of YOY in KZN were highest in southern net installations (Mzamba Beach), in August and September (late-winter and early-spring), when SST"s were cooler, suggesting that pupping grounds are close to the Eastern Cape (Cliff *et al*., 1989, 1996a). Algoa Bay has been proposed as a nursery habitat for YOY white sharks (Dicken, 2008), which were conspicuous inshore in summer months (Dicken and Booth, 2013), but uncommon at Bird Island in winter, when larger sharks were present (Dicken *et al*., 2013).

Both YOY and juvenile white sharks < 220 cm TL, were absent from the Spencer Gulf, South Australia, which does not appear to be a pupping ground or nursery area (Strong *et al*., 1996). Given that only 1% of sharks were potentially YOY, and 6.8% were sized < 249 cm TL overall, it seems unlikely that sharks are using Seal Island as a pupping or nursery area either. However, the presence of particularly small white sharks at Seal Island does suggest some degree of habitat overlap of life history stages, and that recruitment of juvenile sharks into aggregation sites associated with seal colonies, occurs early in life and at small size. This likely accounts for marine-mammal prey remains found in stomach contents of small white sharks< 250 cm TL, examined from the KZN nets (Cliff *et al*., 1989).

Sharks sized 250–299 cm TL constituted 20.8% of the population at Seal Island, and the most commonly encountered size class of shark at Dyer Island and Struisbaai, comprising 33% of all sightings (Ferreira and Ferreira, 1996). In Mossel Bay, 87% of sharks sighted were sized 175–324 cm TL, suggesting that this area acts as an interim nursery "grow-out" area for juvenile and adolescent white sharks (Ryklief, 2012). Sharks < 300 cm TL, comprised 60.3% of sightings at Bird Island (Dicken *et al*., 2013), which was not dissimilar, albeit slightly lower, than in Mossel Bay. However, in stark contrast, 27.6% of the population was sized < 299 cm TL, while 72.4% were sized> 300 cm TL at Seal Island, which strongly supports previous findings that large white sharks are more commonly encountered in False Bay, compared to other South African sites (Kock and Johnson, 2006). Strong *et al*. (1996) reported 17% of sharks were sized 250–299 cm TL in South Australia, with few juvenile sharks encountered at this length off Central California (Chapple *et al*., 2011) or at Guadeloupe Island (Domeier, 2012).

Sharks sized 350–399 cm TL constituted 10.4% of the identified population at Seal Island, and 17.0% of all sightings at Dyer Island and Struisbaai (Ferreira and Ferreira, 1996). Frequencies of sharks in this size class in both South African studies were low compared to South Australia, where they constituted 33% (Strong *et al*., 1996). This suggests that large white sharks are more commonly encountered in the Spencer Gulf. Sharks sized > 450 cm TL

constituted 1.6% of the photo-identified population at Seal Island, and similarly, 2% of sightings in Gansbaai and 3% in Struisbaai (Ferreira and Ferreira, 1996). In another study, white sharks > 450 cm TL comprised 1% of sightings in Gansbaai and 2% in False Bay (Kock and Johnson, 2006). No sharks > 450 cm TL were encountered at Bird Island (Dicken *et al*., 2013) and Mossel Bay (Ryklief, 2012), or have been captured in the KZN nets (Wallet, 1973; Cliff *et al*., 1989; Dudley, 2012), expect for one 480 cm TL female (Wallet, 1978). In South Australia, two different studies reported that sharks sized > 450 cm TL constituted 24% (Bruce, 1992), and 12% (Strong *et al*., 1992), with both estimates, independently, higher than for all sites combined in South Africa. This suggests that particularly large, and therefore adult white sharks, are rare within South African coastal waters, and especially females.

At Seal Island, 7% of males were considered mature (at > 350 cm TL) (Cailliet *et al*., 1985, Francis, 1996, Wintner and Cliff, 1999; Malcolm *et al*., 2001). Kock and Johnson (2006) reported that approximately 20% of the sharks sighted in False Bay and Gansbaai were > 360 cm TL, with similar percentages reported for white sharks at this length around Bird Island (Dicken *et al*., 2013). However, these estimates were not sex-specific and included all sharks sighted, and therefore overestimated the percentages of mature males, which are thus likely to be ≤ 7% at Seal Island. Sharks > 450 cm TL, the approximate size-at-maturity for females (Cailliet *et al*., 1985; Francis, 1996; Wintner and Cliff, 1999; Compagno, 2001), constituted 1% at Seal Island and were not encountered in Mossel Bay (Ryklief, 2012) or Algoa Bay (Dicken *et al*., 2013). In addition, Ferreira and Ferreira (1996) reported a conspicuous absence of white sharks > 400 cm TL at Western Cape sites five years following implementation of protective legislation. Furthermore, no catches nor observations of pregnant female white sharks have been recorded anywhere within South Africa and no records exist for catches of mature females in the KZN nets, despite their high intensity fishing effort over last 61 years (Dudley, 2012).

White shark populations off Central California (Chapple *et al*., 2011) and Guadeloupe Island (Nasby-Lucas and Domeier, 2012) comprise subadult and mature sharks, with mature males predominating. Similarly, mature males are conspicuous at the Neptune Islands (Strong *et al*., 1996; Robbins and Booth, 2012). Although Seal Island hosts a similar size composition of white sharks, i.e. primarily large subadult males and females (> 300 cm TL), adults, and especially females, are more frequently encountered in South Australia and off the US West Coast than in South Africa. Robbins and Booth (2012) reported that the sex ratio among subadults at the Neptune Islands was moderately biased towards male relative to female

sharks, but among mature animals was highly skewed towards males. Thus, mature males were highly conspicuous at the Neptune Islands compared to females in the same maturity class, at this male-dominated offshore site (Strong *et al*., 1996). At Seal Island, ratios for subadult and mature sharks were similar to those for the Neptune Islands, in that males were more abundant relative to females in both maturity classes. However, ratios of subadult males were considerably higher than for subadult females at Seal Island, and ratios of mature males were less disproportionate at Seal Island than their counterparts at the Neptune Islands.

Despite white sharks having been protected for over 22 years in South Africa, mature females are rarely encountered anywhere along the coast (1.0–3.0%, Cliff *et al*., 1996a; Ferreira and Ferreira, 1996; Kock and Johnson, 2006; Dudley, 2012; Ryklief, 2012; Dicken *et al*., 2013), including Seal Island and False Bay, where the largest sharks are known to occur within South Africa (Kock and Johnson, 2006). Ferreira and Ferreira (1996) suggested that intensive hunting pressure over three-decades prior to their study could have been a cause of the observed decline. However, from what is known about growth, length and age-at-maturity (Wintner and Cliff, 1999), sufficient time has passed since protection for both sexes to attain adult sizes, assuming that hunting affected the adult stock to such a degree prior to protection (T. Ferreira Pers. comm. cited by Cliff *et al*., 1996a).

This suggests that either mortality rates are high for adult white sharks in this population, particularly females, or perhaps more likely is that mature females seldom occur in South African coastal waters (Dudley, 2012). Data presented in this study strongly support this notion, with large females permanently emigrating from Seal Island as they approached maturity. As such, it seems unlikely that the absence of mature female white sharks at South African sites is solely related to anthropogenic mortality, although this should not be overlooked. It seems more probable, however, that behaviour related to reproductive biology, or some other essential aspects of the female life-cycle, are responsible for the dispersal of mature female white sharks to other habitat. Cliff *et al.* (2000) reported catches of five large white sharks (380–640 cm TL) around Kenya, Zanzibar, Madagascar and Mauritius, and Zuffa *et al*. (2002) reported catches of 32 large specimens (400–600 cm TL) from Kenya, Zanzibar, Madagascar and Reunion. This strongly supports the notion that movements of large white sharks into tropical waters (Bass *et al*., 1975) is related to reproduction i.e. parturition (Compagno, 2001), and is further supported by relatively high catch frequencies of large, mature-sized white sharks, and in two cases, confirmed pregnant females, from both Kenya and Madagascar (Cliff *et al*., 2000; Zuffa *et al*., 2002).

CHAPTER 5

SUPERPOPULATION SIZE AND APPARENT SURVIVAL OF WHITE SHARKS AT SEAL ISLAND

INTRODUCTION

White sharks (*Carcharodon carcharias*) form predictable aggregations (Nasby-Lucas and Domeier, 2012) and where strong fishing pressure exists, high vulnerability to exploitation can result (Zoo, 2004). This creates a complex management scenario that requires robust, base line estimates of population size and survival; two parameters fundamental to the study of population dynamics (Clavel *et al*., 2008). Marine fish populations have traditionally been assessed using fisheries-dependent data, such as catch-per-unit-effort (CPUE) (Cliff *et al*., 1996a; Pine *et al*., 2003; Dudley and Simpfendorfer, 2006), or fisheries-independent data that include research based biomass surveys (Anderson *et al*., 2011). Until relatively recently, demographic studies on white sharks have been restricted to CPUE analyses (Cliff *et al*., 1996a), due to abbreviated observation times (Cliff *et al*., 1996b) and a lack of mark-recapture methods that are suitable for long-term monitoring research of rare and protected marine species. Despite CPUE being one of the most widely used analyses to describe temporal trends in relative abundance (Williams *et al*., 2002), absolute abundance is not possible to estimate and CPUE data are known to be problematic (Pine *et al*., 2003; Maunder *et al*., 2006; Wilson *et al*., 2011). To overcome this limitation, more complicated population dynamics models that utilise mark-recapture data are required. Photo-identification (photo-ID) of natural marks has since provided a non-invasive alternative for mark-recapture studies on white sharks (see Chapter 3), because individuals can be regularly encountered alive over long periods of time (i.e. 22 y Anderson *et al*., 2011) with minimal impact on their behaviour. Various other mark-recapture methods and population models are now widely applied in wildlife management (Seber, 1982; Pollock *et al*. 1990), through studies on population dynamics, life history and both community and evolutionary ecology (Lindberg, 2010). Temporal changes in population size are governed by both demographic (births and deaths) and geographic (immigration and emigration) processes (Lindberg, 2010). Consequently, basic population models are broadly defined into two categories, closed and open, which

differ in their assumptions regarding whether the population is considered to be closed or open to changes in size over time (Pollock *et al*., 1990).

In general, closed models are applied to estimate abundance over short term studies (<3 y), because they assume that births, deaths and movements do not occur throughout the entire study period. Open population models allow adequate time for births, deaths and movements to occur during the „open" sampling interval, as these parameters, in addition to population size, tend to be of primary interest over longer-term studies (>3 y) (Pollock *et al*., 1990).Three generalizations of the basic open model design exist; known-fate, band recovery and live-encounter (Lindberg, 2010). Live-encounter designs are the most appropriate for monitoring populations of vulnerable, rare or protected species, like white sharks. Live-encounter open population models include the Cormack-Jolly-Seber (CJS) (Cormack, 1964; Jolly, 1965, Seber, 1970) and the Jolly-Seber (JS) (Jolly, 1965; Seber, 1965) and its different formulations, such as Schwarz and Arnason"s (1996) POPAN model. The CJS, JS and POPAN models utilise the same live-encounter capture history structure, but the CJS model utilises information on recaptures of marked individuals only, placing emphasis on the estimation of apparent survival (ϕ), whereas population size estimates (N) are of primary interest with JS models (Schwarz and Seber, 1999).

In addition, time-since-marking (TSM) models can be used within the CJS framework, which condition on the relative age of individuals in a sample (i.e. the time elapsed since the individual was first marked), to estimate the relative proportions of residents to transients in the sampled population. Transients are defined as being marked and released, followed by immediate and permanent emigration from the study area. In contrast, residents are defined as being marked and released, and then conditional on surviving between sampling occasions, they return and are available for recapture in a subsequent sampling period with estimable probability. Thus, by definition, transients can never be recaptured and will appear to have died (i.e. they have zero probability of recapture and apparently do not survive), which results in negatively biased estimates of ϕ. By taking transients (*Trans-*ϕ) into account, TSM models can generate unbiased estimates of resident apparent survival probability (*Res-*ϕ), with the direction and magnitude of the bias determined by *Res-*ϕ – *Trans-*ϕ (Pradel *et al*., 1997).

Although population models are particularly useful tools that are capable of estimating a wide range of demographic parameters, their precise, robust and unbiased

estimation requires that several assumptions are satisfied (Letting and Armstrong, 2003). Specifically that (1) marked individuals permanently retain their identifying marks and they remain identifiable for the duration of the study, (2) the study area size is constant and does not change over time, (3) the sampling period is instantaneous relative to the survival interval, (4) recapture probabilities (p) are homogeneous among all marked and unmarked individuals during each sampling occasion, (5) apparent survival probabilities (ϕ) are homogeneous among all marked and unmarked individuals between sampling occasions, and implicit from the above is that (6) all emigration from the population is permanent (Pollock *et al*., 1990). Adhering to these assumptions is crucial to the robust, unbiased estimation of capture probability, apparent survival and population size with JS models (Schwarz and Arnason, 1996).

Six mark-recapture studies have reported estimates of abundance and other demographic parameters for white sharks at various aggregation sites, worldwide. In South Africa, Cliff *et al*. (1996b) analysed conventional tag returns from six recaptures of 73 white sharks tagged off the south and east coasts and used the „closed" Lincoln-Peterson model to estimate population size at 1279 individuals (95% CI, 839–1843), and mortality rates at F = 0.055 year^{-1} (95% CI, 0.015–0.10) and Z = 0.055 year^{-1} (95% CI, 0.42–0.66) with constant survival (α 0.90). More recently, Ryklief (2012) photo-identified 261 white sharks (75.5% transients) over a three-year period at Mossel Bay (M.Bay) and used Schwarz and Arnason"s (1996) POPAN model to estimate superpopulation size at 389 individuals (95% CI, 351–428) and average annual apparent survival probability at ϕ = 0.90. In the most recent study in South Africa, Towner *et al*. (2013) photo-identified 532 different white sharks over a four-year period at Gansbaai (G.Bay) and used the POPAN model to estimate population size at 908 individuals (95% CI, 808–1008); capture probability and apparent survival estimates were not presented.

In the North East Pacific (NEP), Chapple *et al*. (2011) photo-identified 130 different white sharks over a three-year period and attempted to estimate the subadult and adult superpopulation size at 219 individuals (95% CI, 130–275) off Central Californian (C.Calif), USA, but provided no estimates of survival or mortality. Behavioural telemetry data indicated that sharks were unlikely to have dispersed from C.Calif (i.e. assumptions for population closure were met), and Chapple *et al*. (2011) used a closed Bayesian model framework to derive their estimate. At the second site in the NEP, Guadeloupe Island (G.Island), Nasby-Lucas and Domeier (2012) photo-identified 113 different white sharks over a nine-year

period. Sosa-Nishizaki *et al*. (2012) assessed their capture histories using CJS and POPAN models to estimate population size at 120 individuals and high estimates of apparent survival (ϕ = 0.93). In South Australia, Strong *et al*. (1996) used a basic JS model to estimate white shark population sizes at 191.7 (95% CI, 36.5–1612.2) and 18 individuals (95% CI, 3.9–157.6) in their second (January–March, 1990) and third expeditions (August–September, 1990), respectively, to Dangerous Reef (D.Reef), with particularly low estimates of apparent survival (ϕ = 0.2).

Individual heterogeneity arising from shark behaviour (transience and temporary emigration) and/or limitations with methods used to attract (i.e. baiting and trap responses) and sample individuals (i.e. inadequate capture technique), can violate assumptions of the CJS and JS models on many levels. For example, violation of assumption 4 (i.e. heterogeneous capture probabilities) occurred in two studies (Strong *et al*., 1996; Ryklief, 2012), and failure of assumption 5 (i.e. heterogeneous apparent survival probabilities) occurred in these two studies as well as one other (Towner *et al*., 2013). Thus, violation of model assumptions seems likely to occur to varying degrees in most mark-recapture studies on white sharks that have used basic closed and open population models. Therefore, it is crucial to consider heterogeneity that may arise from these various sources and the extent and direction of any biases that may be introduced into parameter estimates. Despite these limitations, open population models remain the only viable option for live-encounter data and do provide extremely useful tools to assist with conservation management strategies (Pollock *et al*., 1990; Schwarz and Seber, 1999; Sandercock, 2006; Lindberg, 2010).

However, despite such great advances in recent decades with mark-recapture methods and modelling techniques, global superpopulation size remains unknown for white sharks, regional population sizes are uncertain and local population size estimates are absent for several major aggregation sites, such as Seal Island (S.Island), False Bay (F.Bay). Therefore, in this Chapter, data are presented for CJS-TSM models to detect bias in estimates of resident apparent survival probability by taking transients into account, and the JS POPAN model is used to estimate superpopulation size (N), as well as annual probabilities of capture (p), apparent survival (ϕ)and permanent entry (β) of white sharks into the monitored population at S.Island. Estimates are discussed in relation to open population model assumptions, white shark biology, behaviour and life-history, as well as findings from other studies, to provide a pertinent demographic assessment of *C. carcharias* at this important aggregation site.

MATERIALS AND METHODS

Data available

Capture histories were compiled from dorsal fin photo-ID records (Chapter 3) for 303 uniquely identified white sharks (112 male: 111 female: 80 unsexed). Encounter history information was only used for those images collected during photo-ID surveys that took place between May and September, during the peak period of the aggregation at Seal Island, each year between 2004 and 2012. Each capture history included nine binary indicator variables (1 for presence and 0 for absence) corresponding to each year of the study (see Chapter 3).

A suitable model

Closure tests of Stanley and Burnham (1999) and Otis *et al*. (1978) implemented in *Program CloseTest v. 3.2.2* (Stanley and Richards, 2005), showed that the population was open ($p<$ 0.01) and precluded the application of any closed population models. As such, the most suitable live-encounter mark-recapture models available to assess the demographics of white sharks were the CJS model and Schwarz and Arnason"s (1996) superpopulation formulation of the JS model. The CJS model, given s sampling periods, estimates survival between sampling events $\boldsymbol{\varphi} = \{\phi_1, \phi_2, ..., \phi_{s-1}\}$ and probability of capture at each sampling period $\mathbf{p} = \{p_2, p_3, ..., p_s\}$. For a time-dependent saturated model, ignoring any possible confounded parameters, over $s = 9$ sampling periods there are a total of 16 estimated parameters. By contrast, Schwarz and Arnason"s (1996) JS parameterisation, the number of annual births into the population over the duration of the study period is estimated by assuming there is a superpopulation, N, of all animals that will at some time be born together with annual proportions of entry, $\boldsymbol{\beta} = \{\beta_0, \beta_1, ..., \beta_{s-1}\}$, into the population such that $\sum \beta = 1$. In this formulation β_0 would be the number of animals in the population prior to the initiation of sampling. Other parameters estimated are the probability of survival between sampling periods $\boldsymbol{\varphi} = \{\phi_1, \phi_2, ..., \phi_{s-1}\}$ and the probability of capture at each sampling period $\mathbf{p} = \{p_1, p_2, ..., p_s\}$. For a time-dependent saturated JS model, ignoring any possible confounded parameters, over $s = 9$ sampling period there are a total of 25 estimated

parameters as $\beta_0 = 1 - \sum_{t=1}^{s-1} \beta_t$. If all parameters were considered to be temporally-invariant then the model reduces to one with four estimated parameters.

Both the CJS and JS models are flexible and parameters can be estimated as functions of external independent variables, for example sampling effort, *f*, such that capture probability could be modelled as $p_t = \alpha f_t$ with a single estimated parameter α. Similarly, if a population is sex disaggregated with g groups for sexes, then there will be g sets of parameters estimated for the sexes.

Candidate model sets and selection

As statistical models are effectively simplifications of reality, and therefore probably incorrect, it is advocated that a set of competing models be constructed and then assessed against one another (White and Burnham, 1999). In this study, a total of 30 candidate CJS and JS models (summarised in Table. 5.1) were constructed, assuming that parameters may be sex/gender dependent (g), time-dependent (t), time-independent (·) with an interaction between them (g × t), or simply an additive effect (g + t). In addition, time-since-marking (TSM), linear trends over time (T), clustered time parameters (C_t) (where it is assumed that certain time periods are equal), and the number of surveys (*Eff.surv*) or survey hours (*Eff.hrs*) were included in the analyses as covariates.

As both CJS and JS models are fully likelihood-based, all parameter estimates are maximum likelihood estimates (White *et al*., 1999). Therefore, an information theoretic approach was adopted throughout all analyses in this study. Akaike"s Information Criterion (AICc) (Akaike, 1973) adjusted for small sample size (Sugiura, 1978; Hurvich and Tsai, 1989) was used to select the most parsimonious model among all competing candidate models (Burnham and Anderson, 2002). AICc values were converted to QAICc values after *post-hoc* adjustment for overdispersion in the data. Normalised Akaike weights were used to assess the relative support for each model. The difference (Δ) between QAICc model statistics was used to gauge relative plausibility of each model with respect to all other models. If ΔQAICc < 2 then the two models were considered good descriptions of the data, with no strong support for significant differences between models (Burnham and Anderson, 2002).

All models were executed in *MARK v 6.0* (White and Burnham, 1999) with logit-links for *p* and ϕ for both CJS and JS models, and a log-link function used for N and a multinomial-

link for β for the JS model. Confounding parameters were calculated for all models constructed and the model‟s degrees of freedom were adjusted according to the suggestions of White and Burnham (1999). Several Goodness-of-fit (GOF) tests were conducted using *U-CARE v. 2.3.2* (Choquet *et al*., 2005), to assess goodness-of-fit of the full sex/gender-time-dependent CJS model $\{\phi(g \times t)\, p(g \times t)\}$, and to identify potential sources of lack of fit due to overdispersion and heterogeneity among sharks that included transience (Pradel *et al*., 1997) and/or trap-dependence that included trap-happiness or trap-shyness (Pradel, 1993).

Table 5.1.List of hypotheses tested under each model used to estimate annual probability of capture (p), apparent survival (ϕ) and entry of sharks into the population (β), and superpopulation size (N) of white sharks at Seal Island, using the Schwarz and Arnason (1996) parameterisation of the Jolly Seber model.

Model	Hypotheses
ϕ(Ct) ρ(g * Ct) β(g * t)	Apparent survival probability varies by clustered time period, capture probability varies for groups by clustered time period and probability of entering the population varies by group and over time
ϕ(.) ρ(g + t) β(g * t)	Apparent survival probability is constant over time, capture probability varies by group and over time (additive model) and probability of entering the population varies by group and over time
ϕ(T) ρ(g + t) β(g * t)	Apparent survival probability shows a trend over time, capture probability varies by group and over time (additive) and probability of entering the population varies by group and over time
ϕ(Ct) ρ(t) β(g * t)	Apparent survival probability varies by clustered time period, capture probability varies over time and probability of entering the population varies by group and over time
ϕ(.) ρ(t) β(g * t)	Apparent survival probability is constant over time, capture probability varies over time and probability of entering the population varies by group and over time
ϕ(g * Ct) ρ(g * Ct) β(g * t)	Apparent survival probability and capture probability for groups vary by clustered time periods, and probability of entering the population varies by group and over time
ϕ(T) ρ(t) β(g * t)	Apparent survival probability shows a trend over time, capture probability varies over time and probability of entering the population varies by group and over time
ϕ(g) ρ(t) β(g * t)	Apparent survival probability varies by group, capture probability varies over time and probability of entering the population varies by group and over time
ϕ(g) ρ(t) β(t)	Apparent survival probability varies by group, capture probability and probability of entering the population vary over time
ϕ(t) ρ(t) β(t)	Apparent survival probability, capture probability and probability of entering the population vary over time
ϕ(t) ρ(t) β(g * t)	Apparent survival and capture probability vary over time and probability of entering the population varies by group and over time
ϕ(T) ρ(g * Eff.Hrs) β(g * t)	Apparent survival probability shows a trend over time, capture probabilities are dependent on observer effort for each group and probability of entering the population varies by group and over time
ϕ(.) ρ(g * Eff.Hrs) β(g * t)	Apparent survival probability is constant over time, capture probabilities are dependent on observer effort for each group and probability of entering the population varies by group and over time
ϕ(.) ρ(T) β(g * t)DM	Apparent survival probability is constant over time, capture probability shows a trend over time and probability of entering the population varies by group and over time
ϕ(.) ρ(g * T) β(g * t)	Apparent survival probability is constant over time, capture probabilities show a trend over time for each group and probability of entering the population varies by group and over time
ϕ(T) ρ(Eff.Hrs) β(g * t)	Apparent survival probability shows a trend over time, capture probabilities are dependent on observer effort and probability of entering the population varies by group and over time
ϕ(.) ρ(g * Eff.Surv) β(g * t)	Apparent survival probability is constant over time, capture probabilities are dependent on observer effort for each group and probability of entering the population varies by group and over time
ϕ(T) ρ(T) β(g * t)DM	Apparent survival and capture probabilities show a trend over time and probability of entering the population varies by group and over time
ϕ(TSM) ρ(g * t) β(g * t)	Apparent survival probability varies due to a time since-marking effect, capture probability and the probability of entering the population varies by group and over time
ϕ(TSM) ρ(TSM) β(g * t)	Apparent survival and capture probability vary due to a time since-marking effect and probability of entering the population varies by group and over time
ϕ(g) ρ(g) β(g * t)	Apparent survival probability and capture probability vary by group and probability of entering the population varies by group and over time
ϕ(.) ρ(g * t) β(g * t)	Apparent survival probability is constant over time, capture probability and probability of entering the population vary by group and over time
ϕ(.) ρ(Eff.Hrs) β(g * t)	Apparent survival probability is constant over time, capture probability varies with observer effort (number of hours), and probability of entering the population varies by group and over time
ϕ(.) ρ(Eff.Surv) β(g * t)	Apparent survival probability is constant over time, capture probability varies with observer effort (number of surveys), and probability of entering the population varies by group and over time
ϕ(g * t) ρ(t) β(g * t)	Apparent survival probability varies by group and over time, capture probability by time and probability of entering the population varies by group and over time
ϕ(T) ρ(g * t) β(g * t)	Apparent survival probability shows a trend over time, capture probability and probability of entering the population vary by group and over time
ϕ(g) ρ(g * t) β(g * t)	Apparent survival probability varies by group, capture probability and probability of entering the population vary by group and over time
ϕ(g * TSM) ρ(g * t) β(g * t)}	Apparent survival probability varies by group with a time since marking effect, capture probability and probability of entering the population vary by group and over time
ϕ(t) ρ(g * t) β(g * t)	Apparent survival probability varies by time, capture probability and probability of entering the population vary by group and over time
ϕ(g * t) ρ(g * t) β(g * t)	Apparent survival probability, capture probability and probability of entering the population vary by group and over time

RESULTS

Goodness-of-fit (GOF)

Overdispersion

U-CARE tests statistics were summed over groups and used to estimate a variance inflation factor (ĉ = 1.24), which was close to 1.00, indicating minimal lack-of-fit from overdispersion in the data. The inflation factor was applied to the candidate model sets.

General model fit

For the single pooled group analysis (n = 303 individuals), TEST2.CT failed the GOF component test ($\chi^2 = 17.64$, $p < 0.01$), which indicated significant heterogeneity among sharks in their probability of recapture and failure of assumption 4. TEST3.SR indicated that survival probabilities were homogenous among sharks ($\chi^2 = 8.25$, $p = 0.31$), therefore, assumption 5 was not violated. Component TEST2.CL and TEST3.SM passed the GOF tests ($p > 0.05$), although these two tests are of little utility beyond this point in the analysis and are not considered further. Overall, despite TEST2.CT failing the component test, statistics for tests summed over groups, indicated that the fit of the general CJS model to the data was adequate ($\chi^2 = 29.72$, $p = 0.19$). Given the low p-level for TEST3.SR and failure of TEST2.CT for the pooled group analysis, the underlying assumptions of the CJS and POPAN models were only partially supported in the context of the white shark aggregation at Seal Island, and thus warranted further investigation. Therefore, the specific and directional tests were implemented in U-CARE for trap-dependence (TEST2.CT) and transience (TEST3.SR).

The negative test statistic for trap-dependence (TEST2.CT = -3.38, $p < 0.01$) indicated highly significant positive „trap-happy" behavioural responses to capture. Both male (-1.37, $p = 0.17$) and female sharks (-1.84, $p = 0.06$) were trap-happy, evidenced from their negative test statistics. Unsexed sharks demonstrated no trap-dependent behaviour (TEST2.CT = 0, $p = 1$). Transient sharks were detected, evidenced by the positive test statistic (TEST3.SR = 1.71, $p = 0.09$). Males (0.74, $p = 0.46$) were more transient than females (0.25, $p = 0.80$) and unsexed individuals were the most transient of all groups (1.42, $p = 0.16$). Thus, in general, males were both trap happy and transient, females were more trap happy and less transient than males, and unsexed sharks were the most transient and displayed no evidence of trap dependence because they were transient.

Model selection*: CJS model*

From 30 potential candidate models, the 13 parameter clustered time period model 28 $\{\phi(C_t)\ p\ (g \times C_t)\}$ was selected as the most parsimonious model, with optimal balance between precision and fit (Table 5.2).

Table 5.2.Candidate model selection for the Cormack-Jolly-Seber (CJS) model used to estimate apparent survival (ϕ) and recapture probability (p) for white sharks at Seal Island.

Number	Model / Hypothesis	QAICc	ΔQAICc	QAICc Weights	Model Likelihood	Number Parameters
28	$\phi(C_t)\ p(g \times C_t)$	536.54	0.00	0.83	1.00	13
27	$\phi(C_t)\ p(C_t)$	540.12	3.58	0.14	0.17	07
13	$\phi(.)\ p(g + t)$	544.03	7.49	0.02	0.02	11
29	$\phi(g \times Ct)\ p(C_t)$	547.13	10.58	0.00	0.01	15

Table 5.2 summarises the top four ranked CJS models with apparent survival (ϕ) and recapture parameters (p) modelled as constant (·), with additive models (g + t) or customised clustered time periods with ($g \times C_t$) and without group effects (C_t).

CJS time-since-marking (TSM) models

The proportion of resident white sharks in the sample for the single group time-since-marking model $\{\phi(\text{TSM})\ p\ (t)\}$ was 0.63 / 0.72 = 87%, and the proportion of transients was 1 - 0.63 / 0.72 = 13% (Table 5.3). The estimated apparent survival probability for resident sharks was 0.72 (SE = 0.05), and for transient sharks was 0.63 (SE = 0.09). Therefore, the detection of transients in the sampled population negatively biased estimates of resident ϕ by approximately 9% (= 0.72-0.63).

TEST3.SR results supported differing degrees of transience between groups/sexes, therefore, a second model was developed $\{\phi\ (g \times TSM)\ p\ (t)\}$ to estimate the proportion of resident to transient sharks within each group/sex (Table 5.4). The parameter estimates of this TSM model showed that males were more transient than females, and unsexed sharks were highly transient. As a result of transients detected within each group, apparent survival probability estimates were biased negatively for resident male (-7%) and unsexed sharks (-42%), but positively for females (+7%). Reasons for the resulting biases within each group are not clear but could be due to transience and temporary emigration (i.e. trap responses).

Table 5.3.Apparent survival estimates for the time-since-marking model {ϕ (TSM) p (t)}, used to estimate proportions of resident to transient white sharks in at Seal Island. Trans = transient; Res = resident; ϕ = apparent survival probability; SE = standard error; 95% CI (lower – upper).

Parameter	Estimate (SE)	95% CI
ϕ-Trans	0.63 (0.09)	0.45 - 0.78
ϕ-Res	0.72 (0.05)	0.61 - 0.81

Table 5.4.Apparent survival estimates for the time-since-marking model {ϕ (g × TSM) p (t)}, used to estimate proportions of resident to transient white sharks, by sex, at Seal Island. Trans = transient; Res = resident; ϕ = apparent survival probability; SE = standard error; 95% CI (lower – upper).

Parameter	Estimate (SE)	95% CI
ϕ-Trans-♂	0.66 (0.12)	0.40 - 0.85
ϕ-Res-♂	0.73 (0.08)	0.56 - 0.85
ϕ-Trans-♀	0.74 (0.13)	0.44 - 0.91
ϕ-Res-♀	0.67 (0.07)	0.51 - 0.79
ϕ-Trans-U	0.36 (0.11)	0.19 - 0.59
ϕ-Res-U	0.78 (0.11)	0.49 - 0.93

Model selection: POPAN JS model

From 30 potential candidate models, the 40 parameter clustered time-period model # 29{$\phi(C_t)$ $p(g \times C_t)$ $\beta(g \times t)$} was the most parsimonious (Table 5.5). These results supported model rankings in the CJS analysis with clustered time-periods for apparent survival $\phi(C_t)$, and recapture parameters with group effects $p(g \times C_t)$ explaining the data. Group and time-dependence for annual recruitment $\beta(g \times t)$ parameters were strongly supported across all four candidate models.JS model results are summarised in Table 5.6 and illustrated in Figure 5.2.

Table 5.5.Candidate model selection for the Schwarz and Arnason (1996) parameterisation of the Jolly-Seber model, used to estimate apparent survival (ϕ), capture probability (p), probability of entry into the population (β), and superpopulation size (N), for white sharks at Seal Island (refer to Figure 5.1 below for a "flow diagram" representation of the full JS model set).

Number	Model / Hypothesis	QAICc	ΔQAICc	QAICc Weights	Model Likelihood	Number Parameters
29	$\phi(C_t)\ p(g \times C_t)\ \beta(g \times t)$	684.51	0.00	0.98	1.00	40
12	$\phi(.)\ p(g + t)\ \beta(g \times t)$	693.62	9.10	0.01	0.01	39
21	$\phi(T)\ p(g + t)\ \beta(g \times t)$	695.85	11.40	<0.01	<0.01	40
28	$\phi(C_t)\ p(t)\ \beta(g \times t)$	698.65	14.14	<0.01	<0.01	40

Table 5.5 above summarises the top four ranked POPAN (JS) models with apparent survival (ϕ) and recapture parameters (p) modelled as constant (·), time-dependent (t), with additive models (g + t), trends over time (T), and by customised "clustered" time periods with ($g \times C_t$), and without group effects (C_t). Beta (β) parameters were always modelled with full group and time-dependence.

Table 5.6.Parameter estimates for apparent survival (ϕ), capture probability (p), and probability of entry (β), with annual (N) and super-population sizes for the top ranked Schwarz and Arnason (1996) JS model # 29{$\phi(C_t)\ p(g \times C_t)\ \beta(g \times t)$}. ♂ = male; ♀ = female; U = Unsexed; SE = standard error.

Parameter	Year / period	Estimate (SE) ♂	Estimate (SE) ♀	Estimate (SE) U
ϕ	2005	1.00 (0.00)	1.00 (0.00)	1.00 (0.00)
	2006-2008	0.62 (0.06)	0.62 (0.06)	0.62 (0.06)
	2009-2010	0.79 (0.10)	0.79 (0.10)	0.79 (0.10)
	2011-2012	0.53 (0.08)	0.53 (0.08)	0.53 (0.08)
p	2004-2006	0.65 (0.14)	0.80 (0.10)	0.65 (0.21)
	2007-2009	0.19 (0.17)	0.25 (0.07)	0.11 (0.04)
	2010-2012	0.51 (0.12)	0.27 (0.08)	0.13 (0.05)
β	2004-2005	0.19(0.06)	0.19 (0.05)	0.08 (0.04)
	2005-2006	0.18 (0.05)	0.10 (0.03)	0.04 (0.02)
	2006-2007	0.20 (0.12)	0.11 (0.06)	0.10 (0.07)
	2007-2008	0.05 (0.08)	0.13 (0.08)	0.05 (0.08)
	2008-2009	0.00 (0.00)	0.08 (0.08)	0.63 (0.11)
	2009-2010	0.10 (0.07)	0.13 (0.11)	0.00 (0.00)
	2010-2011	0.14 (0.05)	0.24 (0.08)	0.00 (0.00)
	2011-2012	0.10 (0.05)	0.00 (0.00)	0.10 (0.09)
N	2004	6.11 (3.24)	6.26 (2.86)	0.00 (0.01)
	2005	37.57 (9.43)	41.29 (7.68)	21.57 (8.47)
	2006	54.21 (10.54)	43.54 (6.55)	22.52 (6.56)
	2007	67.59 (20.51)	47.71 (12.15)	38.61 (18.66)
	2008	49.61 (14.08)	54.06 (15.44)	36.33 (18.67)
	2009	39.33 (10.76)	57.31 (15.17)	190.68 (56.32)
	2010	48.39 (11.02)	69.07 (19.21)	151.15 (46.61)
	2011	49.35 (11.46	80.81 (20.11)	80.46 (28.61)
	2012	43.43 (10.54)	43.01 (13.66)	69.05 (28.69)
Superpopulation	2004-2012	203.56 (21.93)	223.14 (29.67)	296.67 (79.93)

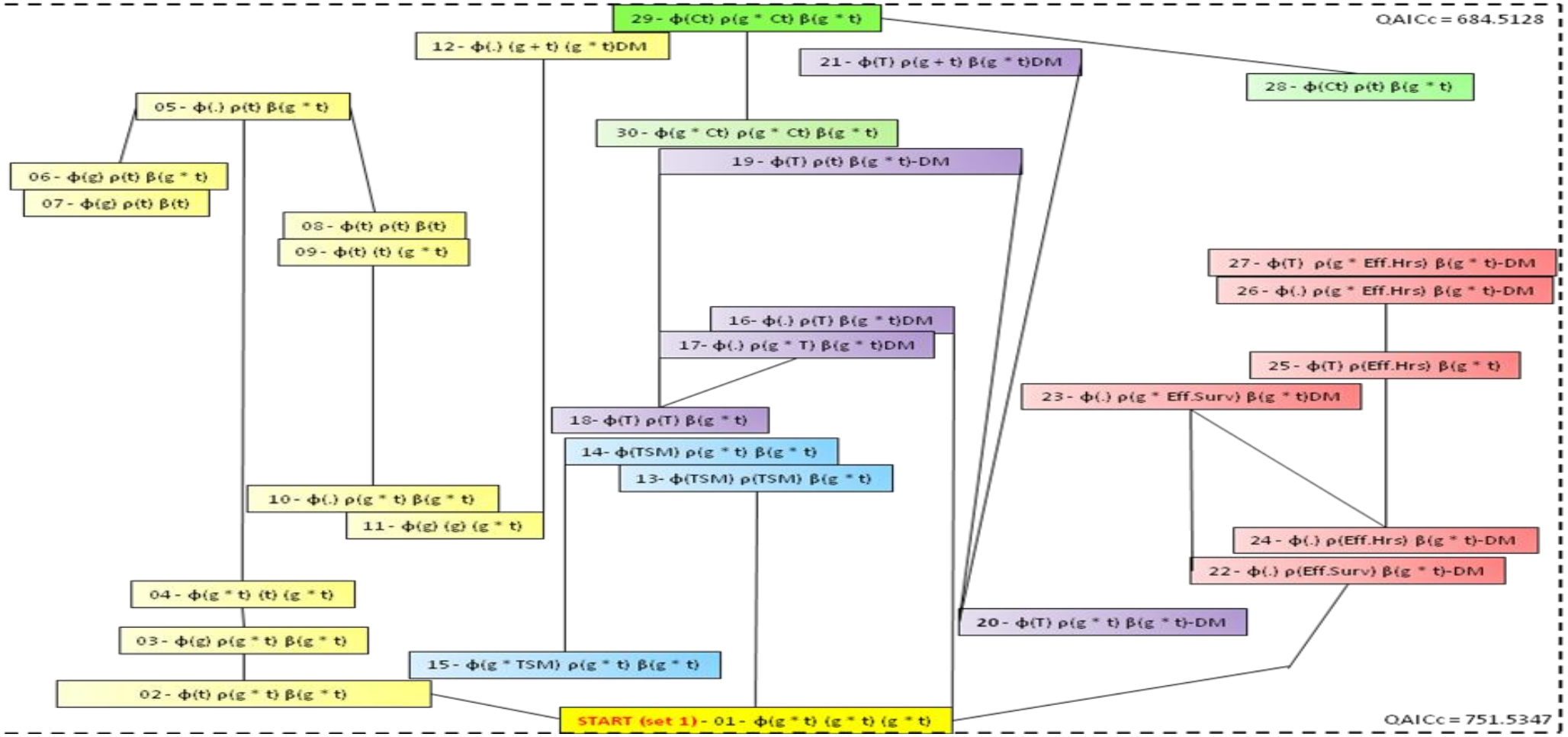

Figure 5.1.Flow diagram representation of the candidate model set (n = 30) used to estimate annual apparent survival (ϕ), capture probability (p), probability of entry into the population (β), and superpopulation size (N) of white sharks at Seal Island, using the Schwarz and Arnason (1996) Jolly Seber model. Yellow = basic parameterisations (t) (g) (·) (g × t); Blue = time-since-marking (TSM) models; Purple = linear trend over time models (T); Red = constrained with effort covariates for the number of surveys (Eff.Surv) and number of survey hours (Eff.Hrs); Green = clustered time periods (C_t).Models are ranked by order or increasing QAICc from top to bottom.

Parameter estimates

Apparent survival probability (ϕ) was homogeneous among sexes and fluctuated across clustered-time-periods $\{\phi(C_t)\}$ i.e. across groups of years, but there was no discernable trend over time (Figure 5.2). Estimates of $\phi(C_t)$ were highest in 2004–2005, declined in 2006–2008 and then increased moderately in 2009–2010. A decline followed in 2011–2012, to the lowest estimate of $\phi(C_t)$ documented in the study i.e. 53% survival.

Estimated capture probability (p) was heterogeneous among sexes and fluctuated across clustered-time-periods $\{p(g \times C_t)\}$. Capture probability estimates were highest in 2004–2006, declined substantially and similarly for all groups in 2007–2009, and were most variable between groups in 2010–2012 (Figure 5.2). In 2004–2006, female $p(C_t)$ was greater than for males and unsexed sharks, which were identical. In 2007–2009, female $p(C_t)$ was highest, followed by that of males and then unsexed sharks, which had the lowest reported $p(C_t)$ estimate in the study ($p_8 = 0.11 \pm 0.04$ SE). In 2010–2012, male $p(C_t)$ increased and was disproportionately high compared to females and unsexed sharks, which did not increase and remained constant and low for the remainder of the study.

The probability estimates of new sharks entering into the population (β) were low, but relatively consistent throughout the study, with an anomalous peak in 2009. Male sharks entered into the population over two noticeable three-year pulses, the first occurred during 2004–2007 and the second in 2010–2012. Male β was relatively consistent within each pulse, but was especially low between pulses when entry of males almost ceased in 2008 and then did cease in 2009. During the second pulse, male β increased but remained lower than estimates from earlier years (Figure 5.2). Female sharks had the most consistent and moderate probabilities of entry into the population, although, like males, two pulses of entry were noted. The first occurred in 2004–2005 and the second in 2010–2011. The highest female β estimate was in 2011, followed by zero entry of females in 2012. However, the penultimate β estimates are inaccurate for all groups due to modelling process of the parameters, and thus cannot be used to infer trends. Unsexed sharks had the lowest rates of permanent entry into the population in all years of the study, except 2009, with a massive pulse of entry of new sharks recorded in the unsexed group.

Annual population size estimates, defined as the number of sharks that visited Seal Island during any year between 2004 and 2012, ranged from 12 to 287 individuals. Annual trends in population size were similar to those trends in sex-specific β estimates i.e. both

gradually and modestly increased each year between 2004 and 2008, and spiked abruptly in 2009 (Figure 5.2), due to increased captures of new sharks, many of which were classed as unsexed. Annual population sizes decreased over the last three years of the study (2010–2012), despite the highest number of surveys (n = 58) being recorded with complete photo-ID effort saturation occurring in 2011.

Annual population size estimates for male sharks showed no distinct trend over time, although they were highest between 2005 and 2007, declined slightly in 2008, and remained comparatively low across the remaining years of the study. Interestingly, male and female population size estimates were both low and identical in 2012. Female annual population size estimates consistently increased with each consecutive year and reached a maximum in 2011 (81 ± 20 SE). Female population size declined in 2012, and the estimate was comparable to those of females in 2005 and 2006. Unsexed shark annual population size estimates were low compared to males and females in 2004–2008 (range = 0–39 individuals). However unsexed shark population size dramatically increased in 2009 (191 ± 56 SE) and remained relatively high in 2010, with an associated increase in captures and the addition of many new sharks to the study (see Chapter 4). However, despite effort being high, unsexed shark population size estimates decreased in 2011 and 2012, like those of male and female sharks, which suggests relatively low recruitment of new individuals into the study population in later years. The superpopulation size estimate, defined as the total number of white sharks that visited Seal Island between June 2004 and September 2012, was 723 ± 132 SE individuals. Respective superpopulation size estimates for male, female and unsexed sharks were 204 ± 22 SE, 223 ± 30 SE and 297 ± 80 SE individuals (Figure 5.2).

Initially, this trend was thought to be associated with increased photo-ID effort and proficiency, particularly during periods of increased immigration. However, it should be noted that annual numbers of surveys (*Eff.surv*) and survey hours (*Eff.hrs*) were modelled as covariates in the analyses (Table 5.1), although none of these models were strongly supported (Table 5.5 and illustrated in Figure 5.1). As a result, models were developed wherein clustered-time-periods (C_t) were modelled, independently, with and without group effects for ϕ and p parameters, to account for any differences in observer ability or variability in effort across groups (i.e. clusters) of years. Model 29$\{\phi(C_t)\ p(g \times C_t)\ \beta(g \times t)\}$, was most strongly supported and generated the most parsimonious description of data (Table 5.5). Thus, all attempts were made through modelling covariates and Ct periods, to account for annual variability in effort and/or observer effects.

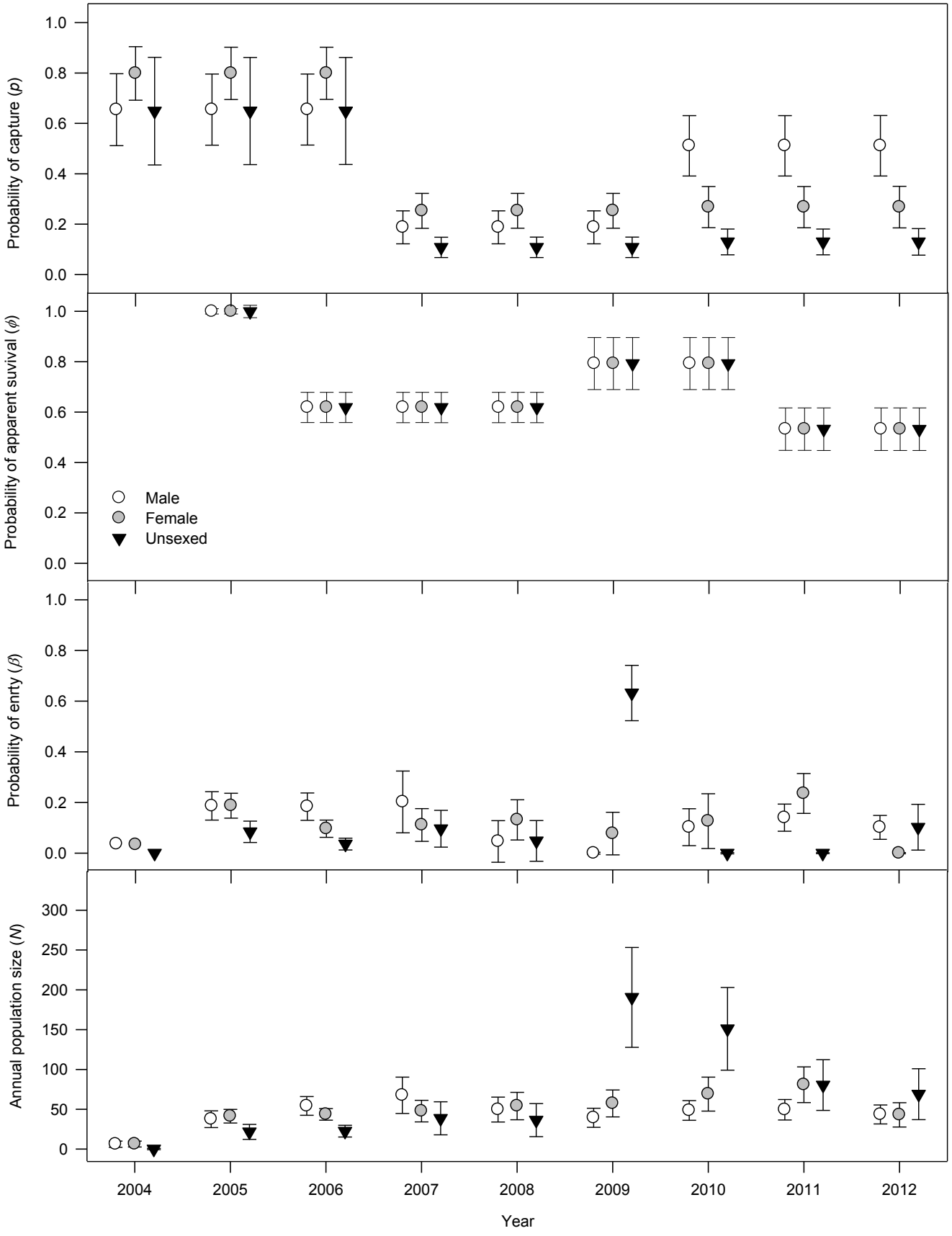

Figure 5.2.Annual estimates for probabilities of capture (p), apparent survival (ϕ) and entry of white sharks into the population (β) at Seal Island, and annual population sizes (N), by sex.

DISCUSSION

Seven mark-recapture studies, including this study, have presented population size and other demographic estimates for white sharks at various aggregation sites, worldwide, and all have achieved this using basic „closed" or „open" population models. Closed models have included the Lincoln-Peterson estimator (Cliff *et al*., 1996b) and more recently a closed Bayesian model framework (Chapple *et al*., 2011), whereas most other studies have used live-encounter open population models, such as the Cormack Jolly Seber (CJS) (Sosa-Nishizaki *et al*., 2012; current study) and the Jolly Seber (JS) (Strong *et al*., 1996), or its different formulations, such as Schwarz and Arnason"s (1996) POPAN model (Ryklief, 2012; Sosa-Nishizaki *et al*., 2012; Towner *et al*., 2013; current study).

The accuracy of estimates derived using these models are questionable, however, for when capture probabilities are low and/or heterogeneous and movements of individuals are prolific within or from the population, mark-recapture analyses based on live-encounter data tend to lose power, which can often result in violation of model assumptions and biased and imprecise parameter estimates (Kendall *et al*., 1995).Therefore, it is important to identify biological, behavioural and methodological factors that contribute to variable detection probabilities (Willson *et al*., 2011). This can often improve precision in parameter estimation and perspective in the accuracy of estimates, and thereby ensures a relevant assessment of a species" demographics (Bailey *et al*., 2004b, 2004c). Therefore, before the parameter estimates presented in this study should be accepted as "truth", and thus before they can be used to assess the abundance and demographics of white sharks at Seal Island (S.Island), biological, behavioural and methodological factors and other potential sources of heterogeneity, should be assessed in relation to CJS and JS model assumptions.

Assumption 1 requires that marked individuals permanently retain their identifying marks, and they are consistently available for detection throughout the study period. This is a critical shared assumption of all mark recapture studies, and its" violation can result in decreased precision in parameter estimates, such as underestimates of recapture probability (Pollock, 1982b) and overestimates of abundance (Pollock *et al*., 1990). The stringent image grading protocol, described in Chapter 3, reduced this source of heterogeneity by excluding poor quality images and the potential for false-positive detections of sharks from misidentification of dorsal fins. In addition, Anderson *et al*. (2011) showed that natural marks, such as notches, were stable on white shark dorsal fins over periods of at least 22

years. Therefore, misidentification of sharks was unlikely to have occurred during this nine-year study or in many other photo-ID studies of similar (Sosa-Nishizaki *et al*., 2012) or shorter duration (Chapple *et al*., 2011; Ryklief, 2012; Towner *et al*., 2013). However, both Cliff *et al*. (1996) and Strong *et al*. (1996) used conventional tag recaptures/resightings, and although Strong *et al*. (1996) reported no tag losses during their study, conventional streamer tags are generally inappropriate for longer term studies on white sharks (Anderson *et al*. 2011) due to fouling, misidentification, shedding and low recapture rates of tags.

Assumption 2 requires that the study area size remains constant and does not change over time. This is important because individual capture probabilities can vary spatially and temporally due to changes in trap position and variable sampling intensity across sites, as individuals move between well and under-studied sites (Buckland, 1990). Thus, assumption 2 is important because it ensures that capture probabilities are homogeneous among individuals and so ensures that assumption 4 is not violated, which could occur if sampling effort is uneven spatially and sharks are over- and under-sampled as a result of movements between sites, when research activities might or might not be in progress. Baiting activities were always conducted in the direct vicinity of the seal colony and the study area size was constant at S.Island (see Chapter 2). Therefore, it is unlikely that this assumption was violated in this study based at a single aggregation site.

However, this source of heterogeneity is likely to arise further when white sharks show preferences for specific aggregation sites but do not frequent other sites throughout the range of the entire population being assessed. For example, Jorgenson *et al*. (2010) demonstrated site-specificity of white sharks for aggregation sites off the Central Californian (C.Calif) coast, which included the Southeast Farallon (SEFI) and Año Nuevo Island"s (ANI) and Tomales Point (TP). Chapple *et al*. (2011) attempted to estimate "C.Calif superpopulation size" using dorsal fin photo-ID data collected from SEFI and TP only. However, because data were excluded from ANI there was likely to have been an unknown proportion of the C.Calif superpopulation that was permanently unavailable for capture at SEFI and at TP, assuming such strong fidelity of sharks. Thus, it seems likely that Chapple *et al*. (2011) underestimated the C.Calif superpopulation size.

What is more, as a result of site-specific behaviour, recapture heterogeneity among sharks was likely to have arisen as a consequence of where they were originally sampled. For example, a SEFI-specific shark would have a different probability of recapture at TP (i.e. zero), than a TP-specific shark at TP, and recapture probabilities would be heterogeneous, in

theory. Thus, capture heterogeneity was likely to have been introduced into Chapple *et al.*'s (2011) study due to variable sampling effort across sites and exclusion of data from ANI.

Assumption 3 requires that all sampling periods are instantaneous relative to the survival interval. This allows sufficient time for mixing of marked and unmarked individuals between „open" sampling intervals, and so ensures homogeneous recapture probabilities among individuals during each sampling occasion (Pollock *et al.*, 1990). Consequently, assumption 3 is also an important prerequisite for assumptions 4 and 5. At S.Island, sharks were instantaneously photographed and released alive on each occasion, within a restricted five-month annual sampling period (May–September), which was shorter than the annual survival interval of approximately seven months (October–April). Given that white sharks dispersed from S.Island each year in September in this study (see Chapter 4), and other studies have shown that they regularly undertake coastal and transoceanic migrations from South Africa (Bonfil *et al.*, 2005; Kock and Johnson, 2006; Ocearch Shark Tracker, unpublished data), these behaviours should have further ensured thorough mixing of sharks and that recapture probabilities were homogeneous among them between years. Thus, it is unlikely that assumption 3 was violated in this study.

Assumption 4 requires that probabilities of recapture (p) are homogeneous among all marked and unmarked individuals during each sampling occasion. Violation of this assumption will occur when recapture probabilities of marked individual's are inflated over the capture probabilities of newly encountered unmarked individual's. This is important because the process by which unmarked individuals, considered to be a random sample of all unmarked individuals in the population (Cooch and White, 2012), are marked and released into the population, is essential for robust estimation of population size with JS models (Schwarz and Seber, 1999). For example, if the proportion of marked individuals in the sample is overestimated, while the proportion of unmarked individuals is underestimated, this can negatively bias estimates of population size (Nichols *et al.*, 1984; Pollock *et al.*, 1990; Bailey *et al.* 2004b) and positively bias estimates of ϕ (Sandercock, 2006).

Capture heterogeneity is likely to exist among individuals in all mark-recapture studies at some point and this assumption is seldom met as a result (Pollock *et al.*, 1990), and particularly in studies on bait-attracted or elusive wildlife species (Willson *et al.*, 2011). Capture probabilities can vary spatially and temporally among individuals or between demographic groups and can arise from differing amounts of time spent by individuals/groups within a study area (i.e. as a result of differing environmental conditions),

or from changes in trap position and variable sampling intensity across sites (Buckland, 1990). Capture probabilities can also vary among demographic groups due to behavioural differences between age cohorts, sexes or reproductive classes (Buckland, 1990, Willson *et al*., 2011), and can also arise among individuals or groups of animals from trap-dependent behaviour (i.e. trap happy or trap shy responses), based on previous experiences with capture methods or baited traps (Willson *et al*., 2011).

In this study, probabilities of recapture varied considerably across years and among sexes, particularly in later years (2010–2012). Low female recapture probabilities from 2007–2012 were consistent with large, subadult females permanently emigrating from the population (see Chapter 4), whereas males were conspicuous in 2010–2012 and regularly encountered with an increased probability of recapture. Both male and female white sharks exhibited „trap-happy" responses, although females were particularly trap-happy, which was attributed to their presence more consistently across months than males, and hence being available for detection more often than males (see Chapter 4).This introduced one source of capture heterogeneity and contributed to violation of assumption 4 in this study, demonstrated by failure of TEST2.CT (U-CARE).

Unfortunately, parameter estimates other than population size, were not presented for white sharks in Gansbaai (G.Bay) (Towner *et al*., 2013) and a comparison could not be made to the demographic estimates presented in this study for p, ϕ and β parameters. However, Towner *et al*."s (2013) goodness-of-fit (GOF) TEST2 (RELEASE) results showed that capture probabilities were homogeneous among sharks (i.e. assumption 4 was not violated), which contrasts with the findings in this study. Although sexes were not specified in Towner *et al*."s (2013) study, if capture heterogeneity had occurred, it would have been detected among individual capture histories, regardless of sex. Thus, it is surprising that capture heterogeneity was not detected considering that sampling occurred throughout the year at two distinct sites within G.Bay, inshore at Joubert"s Dam (J.Dam) and offshore at Dyer Island (D.Island), and within periods of sexual segregation in spring-summer, when males are typically rare inshore (Johnson, 2003; Kock *et al*., 2013). Therefore, it seemed realistic to have hypothesised that female recapture probabilities would be greater than for males because females were potentially available for detection, in theory, up to 50% more of the time than males when inshore.

Similarly, if marked females regularly moved between D.Island and J.Dam and other unmarked females frequented D.Island only, then this could introduce capture heterogeneity

as marked females are over-sampled (i.e. trap-happy) at both sites and unmarked females are relatively under-sampled (i.e. trap-shy) at D.Island. However, this does not appear to have occurred and was not supported by Towner *et al.*'s (2013) GOF test results. Thus, given that capture probabilities were homogeneous, the suggestion is that unmarked females, different to those initially marked at D.Island, were captured inshore at J.Dam, or *vice-versa*, in Towner *et al.*'s (2013) study. This is supported by only 34% of photo-identified sharks (n = 303) being identified both at D.Island and at J.Dam (unpublished photo-ID study by author, 2007–2009), suggesting recruitment of marked, as well as newly encountered unmarked females into the inshore area.

Given this potential trend, it is interesting that limited evidence from the analysis of Mitochondrial DNA suggests that there are two genetically distinct stocks in South Africa, both common and local (Gubili *et al.*, 2012). However, whether this genetic diversity is related to inshore and offshore movements of female sharks, or subpopulations thereof, remains unknown, but presents a particularly interesting direction for future research. Unfortunately, insufficient data were available to investigate this trend further for female white sharks during the spring-summer aggregation inshore in F.Bay.

Ryklief's (2012) GOF TEST2 (RELEASE) results showed that capture probabilities were heterogeneous among sharks in M.Bay (i.e. assumption 4 was violated), similar to the findings in this study but dissimilar to those of Towner *et al.* (2013). Ryklief (2012) attributed low capture probabilities to limitations with methods and shark behaviour (i.e. sharks were present, but were either not photographed (e.g. the dorsal fin was not exposed) or images were acquired but were too poor in quality for further analysis). It also seems likely that spatial and temporal variability in sampling effort across several sites (three inshore areas and one seal colony) might have resulted in low capture probability estimates for certain sharks that resided in or moved between under-studied areas (i.e. trap-shy). However, it seems that because capture probabilities were heterogeneous among sharks in M.Bay, that certain marked individuals might have perhaps been over-sampled inshore, manifesting as trap-happy behaviour and inflating recapture probabilities over other unmarked individuals that were less regularly sampled at other sites.

Sosa-Nishizaki *et al.* (2012) showed that probabilities of recapture were homogeneous among white sharks at Guadeloupe Island (G.Island). However, TEST 2 (RELEASE) was close to failing the test ($p = 0.06$), and although this was not statistically significant in that assumption 4 was not violated, it suggested some degree heterogeneity among individuals. When assessed by sex, capture probabilities of male sharks were found to be heterogeneous,

whereas those of females were homogeneous (Sosa-Nishizaki *et al*., 2012). It is clear from Sosa-Nishizaki *et al*.'s (2012) average capture probability estimates that male sharks (p = 0.80 ± 0.03 SE) were detected more often than females (p = 0.53 ± 0.04 SE), which is consistent with males visiting G.Island annually, whereas adult females demonstrated a non-consecutive other-year visitation pattern (Nasby-Lucas and Domeier, 2012).

Assumption 5 requires that apparent survival probabilities (ϕ) are homogeneous among marked and unmarked individuals between sampling occasions. A limitation shared by all basic open models is their inability to distinguish between permanent (transient) or temporary movements and mortalities (Schwarz and Stobo, 1997, Kendall and Bjorkland, 2001; Sandercock, 2006). Consequently, transient and temporary movements are confounded with mortalities during the estimation of apparent survival (hence why ϕ estimates from CJS and JS models are apparent), which can lead to severe negative biases when movements are prolific. In this study, a time-since-marking model (Pradel *et al*., 1997) was used to detect a 9% negative bias in estimates of ϕ as a consequence of transient movements. However, while permanent transient movements can be partially accounted for using TSM models, movements that are temporary cannot, as these would violate assumption 6 (see below).

In this study, ϕ estimates fluctuated across 2–3 y clustered-time-periods (ϕC_t), but showed no trend over time or variation among sexes. Component TEST3.SR (U-CARE) results demonstrated that assumption 5 was not violated (i.e. apparent survival probabilities were homogenous among sharks), whereas failure of TEST3 (RELEASE) showed that apparent survival probabilities were heterogeneous among sharks in M.Bay (Ryklief, 2012) and in G.Bay (Towner *et al*., 2013), and assumption 5 was violated in both studies. At S.Island, 71% of sharks were identified as transients (i.e. permanent emigrants),whereas 29% were residents, which, despite their semi-residential visitation patterns during the preceding 2–3 consecutive years, also emigrated from the population and were rarely recaptured in later years (see Chapter 4). Thus, transient movements of sharks from S.Island were prolific in this study.

Similar to these findings and despite a shorter study period (i.e. 3 y), Ryklief (2012) reported 75% transients in the M.Bay population, suggesting that transient behaviour is common among white shark populations at South African aggregation sites. The influence that sexes had on violation of this assumption in Ryklief's (2012) and Towner *et al*.'s (2013) studies could not be ascertained, however, given that male sharks appear to be more transient than females (Kock and Johnson, 2006; current study), it seems possible that transient male

behaviour, combined with heterogeneous and limited sampling effort at island relative to inshore sites (when females were abundant and males were rare), could have violated the equal survivorship assumption in these two studies. However, despite 71% transience detected for white sharks at S.Island, apparent survival probabilities were homogeneous. Thus, the effect(s) that transients have on violation of assumption 5, if any, are not clear.

At G.Island, Mexico, apparent survival probabilities were homogeneous among white sharks and assumption 5 was not violated (Sosa-Nishizaki *et al*., 2012). Annual average apparent survival probability was high (ϕ = 0.93) and similar to Ryklief's (2012) findings in M.Bay (ϕ = 0.90). It is not surprising that ϕ estimates were high for white sharks at G.Island given that every shark returned and was recaptured in at least one other year (Nasby-Lucas and Domeier, 2012) and had actually survived (i.e. zero transients). Thus, it seems likely that the absence of transients at G.Island resulted in high and relatively unbiased estimates of ϕ, because movements and mortalities were unlikely to have been confounded. However, Ryklief (2012) reported almost identical estimates of ϕ, despite 75% of sharks being classed as transients in M.Bay, which suggests transient movements of sharks did not introduce considerable negative bias.

However, M.Bay has been proposed as a foraging/refuge, nursery grow-out area for juvenile white sharks (Ryklief, 2012), suggesting that individual's could have remained within the area for extensive periods throughout the study as they matured. As a result, recapture probabilities of marked sharks might have been inflated due to increased detection (i.e. trap happy responses) as a consequence of over-sampling at three inshore sites, which might have resulted in capture heterogeneity, failure of assumption 4 and positively biased estimates of ϕ. However, Ryklief (2012) did not assess trap responses or the affect of transients on estimates of ϕ, and this cannot be determined. Although 93% survival is high, it is not unexpectedly high for white sharks, considering they are apex predators, and are thus expected to have high survival rates, and the species is also protected in South Africa, and presumably should suffer relatively low mortality.

In stark contrast to S.Island, M.Bay and G.Island, Strong *et al*. (1996) reported particularly low estimates of apparent survival (ϕ = 0.20) for white sharks at Dangerous Reef (D.Reef). This suggests either that transient and/or temporary movements of sharks were prolific in this Australian study, mortalities were high, or perhaps conventional tagging methods were ineffective at detecting sharks, although Strong *et al*. (1996) noted this was unlikely because 22% of sharks were double tagged and none showed signs of tag-losses.

Mortality rates were high for white sharks in this population at this time, given that four of the tagged sharks (6.0%) were killed during the 2.5 y study period, three within 78 days of tagging (Strong *et al*., 1996). However, in addition to what appears to be relatively high mortality, it also seems more probable that because Strong *et al*. (1996) estimated apparent survival between their second (January–March, 1990) and third expeditions (August–September, 1990) over a short total duration(i.e. a single year), that many of the tagged sharks emigrated from D.Reef preceding their return to commence sampling later in that year (i.e. tagged sharks were not present and could not be detected), which might have resulted in severe negative bias in estimates of ϕ due to the confounding effects of movements and mortalities.

Assumption 6 requires that all emigration from the study area is permanent (Pollock *et al*., 1990). This presents a specific problem because the common scenario in many wildlife monitoring studies, and particularly in those on highly migratory species, like white sharks, is that animal behaviour can lead to temporary immigration and emigration, when individual‟s are repeatedly entering and leaving the study site (Kendall *et al*., 1997). However, "temporary emigration" is the name used to describe a process whereby individuals are affiliated with the population, but they are unavailable for recapture during the sampling interval (Kendall *et al*., 1997). Temporary emigration is a major source of capture heterogeneity and can arise from biological and behavioural factors (e.g. differences among individuals, age-cohorts, life history stages or sexes) or those that are associated with methods (e.g. ineffective capture technique, poor study design, unequal sampling across sites or the use of baited traps) (Bailey *et al*., 2004b; Sandercock, 2011; Willson *et al*., 2011) or interactions between factors thereof.

In a biological/behavioural context, temporary emigration will occur when individual‟s marked as young (age cohorts) emigrate from the population and only return after a delay of several years (Fujiwara and Caswell, 2002). Similarly, if individuals marked as adults skip every other breeding year (i.e. mature females); they would be temporarily unavailable for recapture up to 50% of the time (Viallefont *et al*., 1995; Kendall and Bjorkland, 2001; Schmidt *et al*., 2002; Sandercock, 2006; Sosa-Nishizaki *et al*., 2012). Equally, if individuals move to other areas irrespective of age, sex or maturity (i.e. to maximise foraging opportunities) (Hestbeck *et al*., 1991), or if individuals become trap shy and cease to respond to baiting activities (i.e. routine, active trap avoidance or during hunting of natural prey), they would also be temporarily unavailable for recapture. From a

methodological perspective, despite individual‟s remaining on the study area and potentially being sighted, they might not be captured, and thus would still be considered temporary emigrants. This could occur when sharks behave intractably (i.e. sharks that do not expose their dorsal fins above water cannot be photographed) such that capture methods are inadequate at detecting all individuals homogeneously

As a result of temporary emigration processes, capture heterogeneity is likely to occur in most field studies (Pollock *et al.,* 1990), which is problematic given that assumption 4 is sensitive to heterogeneity, which can often result in biased estimates of N and ϕ. For example, temporary emigration of marked individuals would deflate recapture probabilities, negatively biasing estimates of ϕ and positively biasing estimates of N. Conversely, increased detection of marked individuals (i.e. trap-happy responses) would overinflate recapture probabilities, positively biasing estimates of ϕ and negatively biasing estimates of N (Pollock *et al*., 1990; Kendall *et al*., 1997; Sandercock, 2006). This is complicated further depending on whether temporary emigration patterns are classed as Random or Markovian. A random temporary emigrant randomly leaves and returns on a continual basis (Kendall *et al*., 1997), whereas a Markovian temporary emigrant is highly time-driven (i.e. it effectively „remembers" it has left the study area; Pine *et al*., 2003) and returns punctually based on some time-dependent function (Kendall *et al*., 1997), and thus regularly demonstrates a high degree of site fidelity. Random movements are, however, rarely observed in wildlife populations (Pine *et al*., 2003) and are highly unlikely for white sharks, with strong seasonal trends in site fidelity, interspersed by bouts of temporary emigration to offshore areas, reported for populations off South Africa (Cliff *et al*., 1996a; Pardini *et al*., 2001; Bonfil *et al*., 2005), California (Boustany *et al*., 2002; Weng *et al*., 2007a, 2007b; Jorgenson *et al*., 2010), G.Island (Nasby-Lucas and Domeier, 2012), New Zealand (Bonfil *et al*., 2010) and South Australia (Bruce *et al*., 2006), that are highly indicative of open populations and Markovian temporary emigration patterns. In situations where random temporary emigration occurs, capture probability will be underestimated and the precision of other parameter estimates can be reduced (Kendall *et al*., 1997; Bailey *et al*., 2004b). However, when capture probabilities are low and movements are Markovian, estimates of N and ϕ are both likely to be negatively biased (Pollock *et al*., 1990; Kendall and Nichols, 1995; Zehfuss *et al*., 1999). This sixth and important assumption is regularly overlooked in mark-recapture studies on white sharks.

In this study, annual population size estimates ranged from 12–287 individuals. Annual trends in the probabilities of white sharks entering into the population (β) resembled

annual trends in population size estimates. Both parameters modestly increased each year in 2004–2008, peaked massively in 2009, due to increased captures of new sharks to the study, and then decreased markedly and consistently with each consecutive year in 2010–2012. This was despite sampling effort in 2011 (n = 58 photo-ID surveys) being the highest in all years, which suggested a general decline in abundance in later years (see Chapter 4).

The superpopulation size estimate for white sharks at S.Island was 723 individuals (204 males, 223 females and 297 unsexed sharks). Cliff *et al*. (1996b) estimated population size along the south and east coasts of South Africa at 1279 individuals. However, sharks were not sampled in G.Bay or F.Bay, except for one juvenile female that was tagged and released in F.Bay. Together these aggregation areas in the Southern and Western Cape Provinces form the regional centre of abundance of white sharks in South Africa (Bass *et al*., 1975). Therefore, given that data were excluded from these sites, Cliff *et al*.‟s (1996b) population size estimate cannot be considered, nor was it originally intended, as a national superpopulation size estimate for South Africa. Since Cliff *et al*.‟s (1996) study, Ryklief (2012) has estimated the superpopulation size of white sharks at M.Bay at 389 individuals, and Towner *et al*. (2013) has estimated superpopulation size at G.Bay at 908 individuals.

The population size estimates of Cliff *et al*. (1996b) and Towner *et al*. (2013) were higher than for white sharks at S.Island, whereas Ryklief‟s (2012) estimate for M.Bay was the lowest of all South African studies. This is not surprising given the difference in duration between studies at S.Island (9 y) and M.Bay (3 y), although this does not apply in Towner *et al*.‟s (2013) study with particularly high estimates of abundance over a relatively short period (4 y). However, had sampling occurred in F.Bay (i.e. not only at S.Island) throughout each of the nine years and with similar sampling effort and spatial coverage to Towner *et al*. (2013), it is highly probable that more than 303 sharks would have been captured and the population size estimate would have greatly increased. Therefore, future demographic research on white sharks in F.Bay should aim to sample sharks both inshore and at S.Island. Until this is permitted and carried out with realistic frequency to generate robust mark-recapture data, population size estimates for white sharks at S.Island cannot be considered as reflective of F.Bay, as they are underestimates, and should only be considered as a minimum index of abundance at S.Island only.

Towner *et al*. (2013) concluded that because 16 years had passed since Cliff *et al*.‟s (1996b) study and their estimates were similar, albeit slightly lower in Towner *et al*.‟s (2013) study, that white shark numbers have not recovered from targeted hunting in the 1950‟s and 1980‟s, gill-net and drum-line captures in KZN and from a lack of protection in Mozambique

in light of recent events (Figure 1.1). However, Peschak and Scholl (2006) photo-identified approximately 1000 different white sharks in G.Bay over a nine year period (1997–2006) that spanned the 11 year gap immediately following and preceding the respective studies of Cliff *et al*. (1996b) and Towner *et al*. (2013). Therefore, Peschak and Scholl (2006) identified more sharks during nine years than Towner *et al*. (2013) estimated as the G.Bay superpopulation size over a four-year period, which suggests that abundance was not particularly low in G.Bay and reflective of previous findings. In theory, if Towner *et al*. (2013) had sampled for twice as long (i.e. over eight or nine years), their capture frequencies (n = 532) would have been higher and closer to 1000 individuals identified by Peschak and Scholl (2006).

Given this it seems possible that Towner *et al*.‟s (2013) population size estimate is reasonably accurate for G.Bay (estimated over a four year period), assuming Peschak and Scholl (2006) identified most of the individuals by the end of their study, although this is somewhat unlikely, however. For example, Towner *et al*.‟s (2013) discovery curve did not asymptote, which was similar to the findings at S.Island over nine years (see Chapter 4, Figure 4.10), showing that different sharks were continually recruited into these monitored populations each year over the duration of both studies. Thus, presumably the same principle applied during Peschak and Scholl‟s (2006) study, so it is unlikely that all sharks had been identified, although there are no data to support or refute this. Regardless, it does seem that the population size of white sharks in G.Bay comprises somewhere in estimated region of approximately 1000 individuals (Peschak and Scholl, 2006; Towner *et al*., 2013).

Towner *et al*., (2013) concluded that because G.Bay was a major aggregation area and several other studies have shown connectivity of individual sharks between G.Bay and other sites in F.Bay, M.Bay, KZN and Western Australia (Pardini *et al*., 2001; Bonfil *et al*., 2005; Kock and Johnson, 2006), this therefore allowed for an accurate, national, superpopulation size estimate for South Africa from this single site. However, although certain white sharks are encountered at several sites within South Africa, other sharks appear to be highly selective and demonstrate strict fidelity to specific sites, similar to Jorgensen *et al*.‟s (2010) findings for white sharks off the C.Calif coast. A preliminary comparison of identified sharks from S.Island with a catalogue from G.Bay (2006–2009; Unpublished data), which overlapped three years of Towner *et al*.‟s (2013) study, suggests that no more than approximately 20% of individuals were common to both areas, although this must still be rigorously tested. For example, WS0001 and other well known and particularly large, adult sharks have not been observed at sites other than S.Island, to the best of current knowledge.

Therefore, it seems probable that an unknown proportion of the "South African superpopulation" is permanently unavailable for capture during studies at discrete aggregation sites (see assumption 2). Therefore, Towner *et al.*'s (2013) proposed superpopulation size estimate for South Africa is likely to be inaccurate, and can only be considered representative of white shark abundance in G.Bay. Furthermore, although Towner *et al*. (2013) sampled a large size range of sharks, few adults were encountered, particularly females, further suggesting that their population size estimate is not reflective of the South African superpopulation. Similarly, this theory can be applied to all other abundance estimates presented for white sharks in South Africa, including the current study, given that adult females were rarely encountered at S.Island or in other studies at coastal sites (Cliff *et al*., 1989, 1996a; Ferreira and Ferreira, 1996; Compagno, 2001; Kock and Johnson, 2006; Dudley, 2012; Ryklief, 2012; Dicken *et al*., 2013).

In addition to Jorgensen *et al.*'s (2010) previous findings, Jorgensen *et al*. (2012) demonstrated that white sharks at coastal sites off C.Calif rarely exchanged with sharks from G.Island, although there was one exception, a mature female that migrated from C.Calif to G.Island and then to Baja California, where she might have given birth. Similar region-specific behaviour has been reported for juvenile white sharks off the east and south-western coasts of Australia, with easterly and westerly movements (Bruce and Bradford, 2012) and gene flow (Blower *et al*., 2012) between these two populations restricted to either side of the Bass Strait. While Towner *et al.*'s (2013) population size estimate does show that G.bay has a large number of white sharks and quite probably one of the largest sub-components of the stock in South Africa, their estimate is unlikely to be representative of national abundance given this site-specificity of white sharks.

Thus, data collected for white sharks at discrete aggregation sites are unlikely to be representative of a demographic/geographic scale that is vastly greater than where the data were originally collected. This will arise when superpopulation size is estimated over the entire range of a population, but when sites are excluded or sampling is non-uniform across sites, throughout the known range of that population, as seems to have occurred in Chapple *et al.*'s (2011). Gathering and processing large numbers of images from multiple sites that can be used to generate robust mark-recapture data, presents a massive challenge and undertaking, but a particularly interesting direction for future collaborative research in South Africa (see Chapter 3). Unfortunately, the South African population size estimates presented thus far cannot be combined to assess superpopulation size either. Inevitably, sharks do move

between aggregation sites in South Africa and these movements must be accounted for if absolute abundance is to be estimated accurately.

It is interesting that all four South African population size estimates are (independently) greater than those presented for white sharks at all other well-studied aggregation sites, worldwide. In the NEP, Chapple *et al*. (2011) estimated the subadult and adult white shark population size at 219 individuals over a three-year period. Sosa-Nishizaki *et al*. (2012) estimated the subadult and adult population size at 120 individuals that aggregated at G.Island over a nine-year period. By crudely combining population size estimates for the NEP, permitted in this case due to negligible exchange of sharks between C.Calif and G.Island (Jorgensen *et al*., 2012), the estimated subadult and adult superpopulation size is particularly small at 339 (= 219 + 120) individuals (Chapple *et al*., 2011; Sosa-Nishizaki *et al*., 2012). This suggests that Chapple *et al*.'s (2011) estimate might resemble a large (i.e. 65%), albeit underestimated, proportion of the subadult and adult white shark stock in the region, whereas G.Island has approximately 35% (Sosa-Nishizaki *et al*. 2012). Neither of the NEP estimates included young-of-the-year (YOY) nor many juvenile sharks, although captures of sharks in these size classes in regional fisheries, suggest that their abundance is also low (Weng *et al*., 2007b; Dewar *et al*., 2004). Therefore, even when YOY and juveniles are included, the predictable outcome is that white sharks are still rare compared to other marine apex predators in the NEP (Chapple *et al*., 2011) and extremely low in abundance compared to southern African white shark populations. The combined estimate for the NEP comprised just 36 more individuals than the 303 different white sharks identified at S.Island, and is significantly lower than the estimated superpopulation size at 723 individuals.

Similar to Chapple *et al*. (2011) and Sosa-Nishizaki *et al*. (2012), Strong *et al*. (1996) reported that YOY and juvenile white sharks were absent at D.Reef and estimated low population sizes at 191.7 and 18 individuals, in their second and third expeditions, respectively. Strong *et al*. (1996) reported that the data used to generate these estimates were collected during a 2.5 y period (1989–1991) when sharks were particularly abundant and shark activity was abnormally high. Strong *et al*. (1996) concluded that their estimates represented maximum abundance for a population that was either at the peak of a long cycle, or that was abnormally large due to unknown causes, which is concerning given that the highest estimate is relatively low. Interestingly, 1989 was one of the 4–6 cyclical peak years described by Cliff *et al.* (1996a) for increased catches of white sharks in the KZN net (see Chapter 4). Thus, it seems possible that large-scale meteorological phenomena might have

farther reaching effects on white shark distribution and abundance in areas other than South Africa. More recent abundance estimates are lacking for Australian population(s) and further comparisons could not be made.

It is not clear why abundance differs so markedly between South African sites and other globally recognised aggregation areas, although Strong *et al*. (1996), Chapple *et al*. (2011) and Sosa-Nishizaki *et al*. (2012) all reported estimates for subadult and adult white sharks only, whereas a broader range of sizes, life history stages and general members of the population seem to have been countered at South African sites. This could result from a high degree of habitat overlap as sharks immigrate into other aggregation sites along the coast as they grow out of other areas (see Chapter 4 Discussion). However, given that many of the white sharks encountered at S.Island were subadult and adult males and both juvenile and adolescent females approaching size-at-maturity (see Chapter 4), it seems that S.Island does have a large number of white sharks belonging to similar size classes and life history stages to those present off C.Calif, G.Island and South Australia. However, mature females are perhaps less regularly encountered at coastal aggregation sites within South Africa than at these other sites. Chapple *et al*. (2011) noted that low genetic diversity and a small population size are consistent with a low carrying capacity after an initial founder event from the Western Pacific (Jorgensen *et al*., 2010; Gubili *et al*., 2012). Increased genetic diversity detected within South African populations (Gubili *et al*., 2012) might result in larger population size(s) off South Africa. Alternatively, low abundance might perhaps reflect the impacts of anthropogenic mortality from overfishing or depletion of prey species, such as pinnipeds (Chapple *et al*., 2011), which was also suggested as one potential reason for low abundance of white sharks at D.Reef (Strong *et al*., 1996). The estimates of white shark population sizes in the NEP and off South Australia are alarmingly low.

Intractable shark behaviour, compounded by limitations inherent with mark-recapture methods (surface based dorsal fin photo-ID), compounded by intractable shark behaviour (transience, temporary emigration and trap responses), are likely to have resulted in biased parameter estimates to varying degrees in these studies as a result of violating important model assumptions. For example, failure of assumption 4 occurred in this study and in the studies of Strong *et al*. (1996) and Ryklief (2012), and although failure of assumption 5 did not occur in this study, it did occur in the studies of Strong *et al*. (1996), Ryklief (2012) and Towner *et al*. (2013). However, if assumptions are violated these models may still be used, but it should then be recognized that the resulting estimates are potentially biased and they

should be placed into context with respect to any sources of heterogeneity arising from the study design or behaviours of individuals within the sampled population.

Although capture heterogeneity did not violate assumption 4 in Sosa-Nishizaki *et al.*'s (2012) study, they concluded that it did negatively bias estimates of population size. However, it is generally agreed that population size estimates from JS models can still be used, but they should be interpreted cautiously and should be used as indices of minimum population size only (Krebs, 1990; Marshall *et al.*, 2011; Sosa-Nishizaki *et al.*, 2012). In addition, while population size estimates are useful to identify long term trends, they cannot be used to assess absolute abundance until methods are improved. These findings demonstrate that population size estimates from single sites are not reflective of national superpopulation sizes, but they reinforce the importance and direct requirements of a national photo-ID monitoring program for white sharks in South Africa. Ultimately, these combined data sets will provide the basis for a robust national population estimate, when assessed with appropriate combined (closed and open) population models like the Robust Design (Pollock, 1981). However, the multistate version of this model, the Multi-State Open Robust Design (MSORD) (Schwarz and Stobo, 1997; Kendal and Bjorkland, 2001; Holmberg *et al.*, 2009) can incorporate mark-recapture data from multiple sources (i.e. sampling sites) and generates robust, unbiased estimates of population size, true survival probability (*S*) and temporary immigration and emigration parameters to account for movements of individuals between sites that would otherwise introduce capture heterogeneity(Schwarz and Stobo, 1997).

CHAPTER 6

SYNTHESIS

On a global scale, anthropogenic impacts on species and ecosystems have expanded at alarming rates, highlighting the need to monitor wildlife populations and especially those of vulnerable or threatened species (Willson *et al*., 2011). White sharks are marine apex predators and given their crucial roles in structuring marine ecosystem health and biodiversity, their populations need to be effectively monitored and managed (Chapple *et al*., 2011). The need exists for standardised, non-lethal means of assessing extant populations of these large, enigmatic sharks (Cailliet, 1996; Strong *et al*., 1996). A sound definition of population dynamics is essential to the formulation of effective conservation management strategies (Gubili *et al*., 2012), and this dissertation comprises an important step towards achieving this objective in South Africa. This study generated a comprehensive dataset with a large sample size, which included sightings and photographic data for male, female and unsexed sharks, and implemented several different analyses to assess their demographics. The data presented in this dissertation are, therefore, thought to represent accurately the population biology and behaviour of white sharks at Seal Island.

Photo-ID was used effectively to identify white sharks in Chapter 3. Dorsal fin shapes and natural marks were robust, anatomical features that showed negligible natural change over almost a decade. In Chapter 4, data were presented for 34 months of photo-ID sampling for the period 2004–2012, which comprised 576.92 hours of observations and 1105 shark sightings. Using sightings per unit effort analyses (SPUE) the mean annual sighting rate was 1.87 sharks per hour. Female sharks were sighted more consistently across months than males and remained at the seal colony until later months in spring. Despite such a strong seasonal trend in white shark occurrence, sharks were sighted more infrequently in later years and sighting rates decreased significantly over the nine-year study from a maximum in 2005 and 2006 to a minimum in 2011.

Sexual segregation was not evident for white sharks at Seal Island (1.0: 1.0: 2.3, ♂: ♀: *U*), although inter-annual variability was detected and might have been related to water temperature fluctuations, similar to reports for white sharks in Gansbaai (Towner *et al*., 2013) and at the Neptune Islands (Robbins and Booth, 2012). These South African studies have predominantly sampled juvenile sharks and are likely to have incurred seasonal biases from

high intensity sampling at inshore sites during sexual segregation. It does appear that female white sharks are generally more abundant than males in South Africa, although the sex ratio reported for large white sharks at Seal Island suggests that sex composition of subadult and mature *C. carcharias* in South Africa is equal, assuming that the unsexed group was not biased.

Almost 40% of sharks were photo-identified in this study, and although new sharks were identified annually, sightings, captures and recaptures all decreased, suggesting fewer sharks were recruited into, or returned to, the population. Of the 303 sharks, 71% were „transient", whereas 29% were „resident". The majority (98%) of resident sharks were recaptured in < 3 years, with 35% temporarily emigrating for a year or more before recapture and no differences between male and female sharks. The other 65% of residents were recaptured the following year(s), with females exhibiting fidelity to Seal Island over short time-periods, i.e. 2–3 consecutive years, followed by what appears to have been permanent emigration as they approached maturity (450 cm TL).

Subadult and mature female white sharks initially encountered in 2004–2007 had dispersed from the population around 2008 to 2009 and were rarely recaptured in 2010–2012. Presumably, these female sharks had reached maturity in later years of the study, when photo-ID effort and sampling efficiency had also increased markedly. Therefore, it was unlikely such large adult females (>450 cm TL) would have been missed, which generated further support for the hypothesis that mature females permanently emigrated from the population. Certain males exhibited fidelity over longer time-periods, possibly visiting every year and particularly as adults.

Size-based sexual segregation was not evident, with male and female sharks identified in all size classes. However, few young-of-the-year sharks were present, suggesting that Seal Island is not a pupping ground and/or nursery area. Pupping grounds are most likely to occur between the Eastern (Cliff *et al.*, 1989, 1996a; Dicken, 2008) and Southern Cape(s), with Mossel Bay proposed as one potential "grow-out" area for juvenile white sharks (Ryklief, 2012). The findings of this study support those from previous studies in that large white sharks are more commonly encountered in False Bay compared to other South African sites (Kock and Johnson, 2006), and further supports longitudinal distribution of size classes similar to US shark populations (Casey and Pratt, 1985; Klimley, 1985; Domeier, 2012).

Although aggregation sites around the Western Cape from Struisbaai to False Bay host similar mean sized female sharks, large males were predominantly encountered in winter months at Dyer Island (Ferreira and Ferreira, 1996) and particularly at Seal Island, suggesting

these two sites are critically important to males. This was further supported with 7% of male sharks being classed mature, whereas mature female sharks constituted just 1% of the population. Ratios of males in both subadult and mature life history stages were significantly more abundant than their female counterparts. Despite large mature white sharks of both sexes being present, it seems unlikely that mating occurs during the winter aggregation. It seems more probable that Seal Island provides a crucial provisioning stop-over site, vital to the growth and development of maturing white sharks in southern Africa. Mature and pregnant female white sharks appear to be more frequently encountered around other regions of Africa and the Western Indian Ocean (Cliff *et al*., 2000; Zuffa *et al*., 2002). It therefore seems probable that behaviours related to reproductive biology and to female life history are responsible for driving their dispersal from coastal aggregation sites to other habitat. Alternatively, mortality rates could be high for adult sharks in this population, although it seems more likely that mature females seldom occur in coastal waters (Dudley, 2012).

The capture histories of 303 photo-identified white sharks showed that significant capture heterogeneity among sexes and trap-responses were detected, and the corresponding assumption was violated. Apparent survival probability was homogeneous among sharks and the analogous „survival assumption" had not, therefore, been violated. The superpopulation size was estimated at 723 individuals, with annual abundance estimates ranging from 12–287 individuals. The four abundance estimates presented for white sharks at South African sites (Cliff *et al*., 1996; Ryklief, 2012; Towner *et al*., 2013; current study), were all, independently, higher than population size estimates for all other well-studied international sites (Strong *et al*., 1996; Chapple *et al*., 2011; Sosa-Nishizaki *et al*., 2012), although the two sampled populations in the Northeast Pacific primarily comprised subadult and mature sharks. In contrast, a broader range of sizes and life history stages were sampled along the South African coast, although YOY and adult female sharks were rare and juveniles < 250 cm TL were not particularly common at Seal Island.

Towner *et al*.'s (2013) abundance estimate showed that Gansbaai probably hosts one of the largest sub-components of the South African stock, although their estimate was unlikely to represent national abundance. This was highlighted by site specificity of individual sharks to Seal Island (unpublished data) and of sharks to other sites and/or populations (Blower *et al*., 2012; Bruce and Bradford, 2012; Jorgensen *et al*., 2012; unpublished data). Unfortunately, none of the South African estimates presented thus far can be considered representative of national superpopulation size, nor can these estimates just simply be added together to generate an estimate, limited by permanent and temporary

emigration patterns of sharks that appear to be major behavioural dynamics of populations in South Africa (Ryklief, 2012; current study). Combining these independent photographic datasets in future would provide a strong foundation for a national population estimate. However, this would require that the resultant data are assessed with appropriate population models, such as the Multi State Open Robust Design (MSORD), which take movements of sharks into account (Schwarz and Stobo, 1997; Kendal and Bjorkland, 2001; Holmberg *et al*., 2009).

Apparent survival probabilities were homogeneous among sexes and fluctuated across years between clustered 2 to 3 year periods (ϕC_t). The estimate of ϕ for the period 2010–2012 was the lowest documented throughout the entire study. This was unexpected given that photo-ID effort and proficiency was highest in this later period. Despite the homogeneous survival assumption having being met, transients were detected and constituted the bulk of the sampled populations in Mossel Bay and at Seal Island, i.e. 71–75% (Ryklief, 2012). A TSM model showed a 9% negative bias effect of transient behaviour on estimates of resident apparent survival. It is therefore recommended that future photo-ID mark-recapture studies on white sharks using and CJS/JS models should account for bias introduced from transient sharks using TSM models. The average apparent survival estimate was $\phi = 0.72$, which, in absolute terms, was still unexpectedly low, especially for a population of such large white sharks. These findings suggested that white shark behaviour, i.e. Markovian temporary emigration patterns, were potentially capable of introducing considerable negative bias into estimates of apparent survival. However, the relative importance that emigration processes has on estimates of ϕ can only realistically be disentangled for white sharks with behavioural-telemetry data (Anderson *et al*., 2011). The need therefore exists for combined telemetry/photo-ID studies to facilitate robust estimates of survival taking movements and/or mortality of sharks into account.

Capture probability was heterogeneous among sharks and the corresponding assumption was violated. Both male and female sharks exhibited „trap-happy" responses, females more so than males, whereas unsexed sharks showed no evidence of trap-dependence, and were the most transient of all groups. Females were hypothesised to be either more abundant than males in general, which was not supported by sex ratio data, or more probable was that a systematic behavioural effect predisposed females to higher detection rates than males, which manifested as elevated „trap-happy" responses for females. In general, males were more transient than females, although certain male sharks returned

almost annually and therefore exhibited fidelity over longer time-periods i.e. 4–9 years. Female capture probability was highest in 2004–2006, which then decreased and remained low and constant from 2007–2012, further supporting permanent emigration of females from the population. In contrast, male capture probability increased in 2010–2012, with the recapture of several well known, adult males, and captures of new, previously un-photographed males, thus, males dominated in later years

Life-history hypothesis

The results of this study, in conjunction with previous studies, provide an opportunity to propose the first life-history hypothesis for the South African white shark population. The distribution of large white sharks in South Africa appears to be primarily dictated by foraging ecology of specific life-history stages, with shark total length generally increasing from east to west coasts (Cliff *et al*., 1989, 1996a; Ferreira and Ferreira, 1996; Kock and Johnson, 2006; Dicken, 2008; Laroche *et al*., 2008; Hussey *et al*., 2012; Ryklief, 2012; Smale and Cliff, 2012; Kock *et al*., 2013). Juvenile and adolescent white sharks are widely distributed along the South African coast, which is presumably dictated by sized-based physiological and/or prey requirements, and environmental conditions, such as sea SST (Cliff *et al*., 1996a; Towner *et al*. 2013; Weltz *et al*., 2013), barometric pressure (Dicken *et al*., 2013) and other closely related environmental parameters, like upwelling, which seem to be driven by large scale meteorological phenomena every 4–6 years (Cliff *et al*., 1996a; Towner *et al*., 2013)

Juvenile habitat predominantly occurs between Mossel Bay and KZN, potentially due to the rich diversity of teleost and elasmobranch prey at these sites (Dicken, 2008; Dudley and Cliff, 2010; Ryklief, 2012) but also extends west into Gansbaai and False Bay. As juvenile sharks grow out of adolescence, ontogenetic changes in diet (Tricas and McCosker, 1984) and the high energetic demands of increasing body size (Semmens *et al*., 2013), shift dietary requirements, predatory behaviour and prey selection of juveniles from a piscine diet to one dominated by marine mammals at approximately 300–340 cm TL (Tricas and McCosker, 1984; Cliff *et al*., 1989; Estrada *et al*., 2006; Hussey *et al*., 2012). Consequently, their distribution shifts west into coastal aggregation sites in the Western Cape with associated Cape fur seal breeding-colonies, evidenced by different sharks continually being recruited into these sites from other areas (Towner *et al*., 2013; current study). As they mature, large white sharks return to these sites showing fidelity over periods of approximately three years but as long as nine years, where they hunt juvenile Cape fur seals

over winter months. Consumption of energy-rich prey potentially speeds growth, development and maturation of sharks, and provides a vital source of nutrition to fuel migrations. As large female white sharks approached size at maturity (> 450 cm TL), after having provisioned on pinniped prey for several consecutive years, they dispersed and were rarely recaptured at Seal Island. Thereafter, it is postulated that mature females emigrate from coastal waters of the Western Cape and shift their distribution into pelagic habitat, where they remain for extended periods of time (Bonfil *et al*., 2005; Ocearch Shark Tracker, unpublished data).

Catches of white sharks in the KZN nets were reported throughout the year, but were highest in July and August (Cliff *et al*., 1989, 1996a), coinciding with peak months in shark sighting rates at Seal Island. This supports the hypothesis that seal colonies in the Western Cape form important seasonal provisioning habitat for white sharks in winter months, which facilitates eastward migrations in spring into KZN and Mozambique (Ocearch Shark Tracker, unpublished data). Indirect evidence from shark bite inflicted wounds on manta rays, i.e. > 75% (Marshall *et al*., 2011), suggests *M. alfredi* might be one potential prey species in Mozambique. However, other large predatory sharks are also present, such as tiger (*Galeocerdo cuvier*) and bull sharks (*Carcharhinus leucas*), and are equally likely as potential predators of these rays.

It seems probable that warm sub-tropical and tropical West Indian Ocean waters, its Oceanic Islands (Cliff *et al*., 2000; Zuffa *et al*., 2002), or perhaps raised submarine plateaus like the Chagos Archipelago (Ocearch Shark Tracker, unpublished data) and other submerged features with warm associated SST‟s, present potential candidate sites of reproductive importance for mature and possibly gravid females. Behavioural shifts of mature females into warm water might hasten physiological development of females and embryos and increase reproductive output (Klimley, 1985b; Robbins and Booth, 2012; Domeier, 2012). The findings of Smale and Cliff (2012) are consistent with large sharks preying more often on deep water mesopelagic cephalopods from temperate, sub-tropical and tropical regions, which could account for the switch in forage base of large white sharks, especially pregnant females (Hussey *et al*., 2012), during offshore migrations for extended periods of time, which has been suggested for white sharks in the Northeast Pacific Ocean (Domeier, 2012).

Despite large white sharks being present at Seal Island, the aggregation does not appear to form directly in relation to reproduction, i.e. mating or parturition, nor does this site represent refuging habitat, such as a nursery ground. Whether white sharks mate within coastal waters off South Africa is not known, and there is no direct evidence to suggest that

mating occurs in winter around Seal Island. While, it is possible that other less well-studied areas in the Western Cape, such as De Hoop Nature Reserve, or areas off the Agulhas Bank, might present potential mating sites (Ocearch Shark Tracker; Pers. Obs. during expedition), it is equally plausible that mating occurs outside of South African coastal waters, potentially off Mozambican or Madagascan coastlines, given catch records of large mature male and female white sharks from these regions (Cliff *et al*., 2000; Zuffa *et al*., 2002).

Regardless of where mating occurs, it is postulated that after an approximate 18 to 24 month gestation period spent offshore (Francis, 1996, Domeier, 2012), gravid females immigrate back into coastal waters south of KZN around the Eastern Cape in spring and summer, when female white sharks are known to segregate inshore in other areas (Johnson, 2003; Kock *et al*., 2013), and when YOY white sharks are most frequently encountered in this region (Cliff *et al*., 1989; Dicken, 2008; Dicken *et al*., 2013). Post-partum female white sharks might then either disperse from the coast back into pelagic habitat to forage and rest before mating again (see Domeier, 2012), or perhaps they migrate west to seal colonies to provision on pinnipeds over winter, which might account for why a small proportion of mature female white sharks are still encountered at Western Cape sites. Presumably once mature females migrate back into pelagic habitat they feed predominantly of deep water cephalopods (Smale and Cliff, 2012), which might partially or fully sustain their extended 18-24 month forays offshore during gestation (Domeier, 2012).

CONCLUSION

Sighting rates, captures and recaptures, as well as annual population size and apparent survival estimates all decreased in 2010–2012, and despite effort in 2011 being the highest in all years. This suggested that either mortality rates were potentially high, a specific concern in light of recent shark finning events in Mozambique, or perhaps more likely, given movements and trap dependent behaviours of sharks, which are capable of introducing bias on many levels with CJS and JS models, was that estimates of ϕ were negatively biased. While estimates might be biased they are valuable and may still be used provided biases are acknowledged and ultimately placed into context with the behaviour of study subjects. The reproductive biology and behaviour of white sharks remains particularly challenging to assess and therefore knowledge remains rudimentary in this regard at present. The estimates presented in this dissertation, regardless of potential bias, do form important base-line data for this aggregation of large white sharks, and contribute another fundamental step towards building a comprehensive view of their population dynamics in South Africa. These base-line data will enable quantitative assessment of the future effects of anthropogenic mortality or natural fluctuations within this population and potentially between others. This study has also provided new insights into biology and behaviour and has developed a new life-history hypothesis and dispersal mechanism for mature white sharks in southern Africa. These insights might hopefully assist in directing future research and provide information for the development of both national and international management plans for white sharks.

CHAPTER 7

REFERENCES

Ainley, D., Strong, C., Huber, H., Lewis, T., and Morrell, S. 1981. Predation by sharks on pinnipeds at the Farallon Islands. Fisheries Bulletin, 78: 941–945.

Ainley, D., Henderson, R., Huber, H., Boekelheide, R., Allen, S. and McEltroy, T. 1985.Dynamic of white shark/pinniped interactions in the Gulf of the Farallones. Memoirs of the Southern California Academy of Sciences, 9: 109–122.

Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle. In: Petrov, B., and Csaksi, F. (Eds). Second international symposium on information theory. Akademiai Kiado, Budapest, Hungary. Pp: 267–281.

Anderson, S., and Goldman, K. 1996. Photographic evidence of white shark movements in Californian waters. California Fish and Game, 82: 182–186.

Anderson, S., Henderson, R., Pyle, P., Ainley, D., and Klimley, P. 1996. White shark reactions to unbaited decoys. In: Klimley, P., and Ainley, D. (Eds). Great white sharks. The biology of *Carcharodon carcharias* Pp: 223–228.

Anderson, S., Chapple, T., Jorgensen, S., Klimley, P., and Block, B. 2011.Long-term individual identification and site fidelity of white sharks, *Carcharodon carcharias*, off California using dorsal fins. Marine Biology, 158: 1233–1237.

Bailey, L., Simons, T., and Pollock, K. 2004a. Comparing population size estimators for Plethodontid salamanders. Journal of Herpetology, 68: 1–13.

Bailey, L., Simons, T., and Pollock, K. 2004b. Estimating detection probability parameters for plethodon salamanders using the robust capture–recapture design. Journal of Wildlife Management, 68: 1–13.

Bailey, L., Simons, T., and Pollock, K. 2004c. Comparing population size estimators for plethodontid salamanders. Journal of Herpetology, 38: 370–380.

Baillie, J., Hilton–Taylor, C., and Stuart, S., 2004. IUCN Red List of Threatened Species: A global species assessment. World Conservation Union, Gland, Switzerland, Pp191.

Bascompte, J., Melian, C., and Sala, E. 2005. Interaction strength combinations and the overfishing of a marine food web. Proceedings of the National Academy of Science, 102:5443–5447.

Bass, A., D'Aubrey, J., and Kistnasamy, N. 1975. Sharks of the east coast of southern Africa. V. The families Odontaspididae, Scapanorhynchidae, Isuridae, Cetorhinidae, Alopiidae,

Orectolobidae and Rhiniodontidae. Oceanographic Research Institute, Investigatory Reports, 39: 22–26.

Bass, A. 1978.Problems in studies in the southwest Indian Ocean. In: Hodgson, E. and Mathewson, R. (Eds). Sensory Biology of Sharks, Skates and Rays. US Office of Naval Research, Arlington, VA, Pp: 545–594.

Baum, J., Myers, R., Kehler, D., Worm, B., Harley, S., and Doherty, P. 2003. Collapse and conservation of shark populations in the Northwest Atlantic. Science, 299: 389–391.

Baum, J., and Myers, R. 2004. Shifting baselines and the decline of pelagic sharks in the Gulf of Mexico. Ecology Letters, 7:135-145.

Bonfil, R. 1994.Overview of world elasmobranch fisheries. FAO Fisheries technical paper 341, Rome, Pp 1–119.

Bonfil, R., Meyer, M., Scholl, M., Johnson, R., O'Brian, S., Oosthuizen, H., Swanson, S., Kotze, D., and Patterson, M. 2005. Transoceanic migration, spatial dynamics, and population linkages of white sharks. Science, 301: 100–103.

Bonfil, R., Francis, M., Duffy, C., Manning, M., and O'Brien, S. 2010. Large-scale tropical movements and diving behaviour of white sharks, *Carcharodon carcharias,* tagged off New Zealand. Aquatic Biology, 8: 115–123.

Boustany, A., Davis, S., Pyle, P., Anderson, S., LeBoeuf, B., and Block, B. 2002. Expanded niche of white sharks. Nature, 415: 35–36.

Brooks, E., Sloman, K., Sims, D., and Danylchuk, A. 2011. Validating the use of baited remote underwater video surveys for assessing the diversity, distribution and abundance of sharks in the Bahamas. Endangered Species Research, 13: 231–243.

Bruce, B. 1992. Preliminary observations on the biology of the White Shark, *Carcharodon carcharias*, in South Australian waters. Australian Journal of Marine and Freshwater Research, 43: 1–11.

Bruce, B. 2009.The biology and ecology of the white shark, *Carcharodon carcharias*. In: sharks of the open ocean: Biology, fisheries and conservation, Camhi, M., Pikitch, E., and Babcock, E. (Eds). Oxford, UK: Blackwell Publishing, Pp: 69–81.

Bruce, B., and Bradford, R. 2008. Spatial dynamics and habitat preferences of juvenile white sharks: identifying critical habitat and options for monitoring recruitment. CSIRO Marine and Atmospheric Research. Final Report, June 2008, Pp: 1–71.

Bruce, B., and Bradford, R. 2011. The effects of berleying on the distribution and behaviour of white sharks, *Carcharodon carcharias*, at the Neptune Islands, South Australia. CSIRO Wealth from Oceans Flagship. Marine and Atmospheric Research, Hobart. Final report. 1–40.

Bruce, B., and Bradford, R. 2012. Habitat use and spatial dynamics of juvenile white sharks, *Carcharodon carcharias*, in eastern Australia. In: Global perspectives on the biology and life history of the white shark (Ed. Domeier, M), 225–253.CRC Press, Boca Raton, Florida.

Bruce, B., Stevens, J., and Bradford, R. 2005. Site fidelity, residence times and home range patterns of white sharks around pinniped colonies. Final Report to the Australian Government Department of the Environment and Heritage. CSIRO Marine and Atmospheric Research, Hobart.

Bruce, B., Stevens, J., and Malcolm, H. 2006. Movements and swimming behaviour of white sharks (*Carcharodon carcharias*) in Australian waters. Marine Biology, 150(2): 161–172.doi:10.1007/s00227–006–0325–1.

Buray, N., Mourie, J., Planes, S., and Clua, E. 2009. Underwater photo–identification of sicklefin lemon sharks, *Negaprion acutidens*, at Mooea (French Polynesia). Cybium, 1: 21–27.

Burnham, K., and Anderson, D. 2002. Model selection and multimodel inference: A practical information– theoretic approach. New York, NY: Springer–Verlag.

Cailliet, G. 1996.An evaluation of methodologies to study the population biology of white sharks. In: Klimley, P., and Ainley, D. (Eds). Great White Sharks: The Biology of *Carcharodon carcharias*: Pp 415–416.

Cailliet, G., Natanson, L., Weldon, B., and Ebert, D. 1985. Preliminary studies on the age and growth of the white shark *Carcharodon carcharias*, using vertebral bands. Memoirs of the Southern California Academy of Sciences, 9: 49–60.

Calambokidis, J., Steiger, G., Ellifrit, D., Troutman, B., and Bowlby, C. 2004. Distribution and abundance of humpback whales (*Megaptera novaeangliae*) and other marine mammals of the northern Washington coast. Fisheries Bulletin, 102(4): 563–580.

Casey, J., and Pratt, H. 1985. Distribution of the white shark, *Carcharodon carcharias*, in the western North Atlantic. Southern California Academy of Science Memoirs, 9: 2–14.

Castro, A., and Rosa, R. 2005. Use of natural marks on population estimates of the nurse shark, *Ginglymostoma cirratum*, at Atol das Rocas Biological Reserve, Brazil. Environmental Biology of Fishes, 72: 213–221.

Chapman, D., Abercrombie, D., Douady, C., Pikitch E., Stanhope, M., and Shivji, M. 2003. A streamlined, bi–organelle, multiplex PCR approach to species identification: application to global conservation and trade monitoring of the great white shark, *Carcharodon carcharias*. Conservation Genetics, 4: 415–425.

Chapple, T., Jorgensen, S., Anderson, S., Kanive, P., Klimley, P., Botsford, W., and Block, B. 2011. A first estimate of white shark, *Carcharodon carcharias*, abundance off Central California. Biological letters, 7: 581–583.

Choquet, R., Reboulet, A., Lebreton, J., Gimenez, O., and Pradel, R. 2005b.U–CARE 2.2 Users Manual. CEFE–CNRS, Montpellier, France. http://ftp.cefe.cnrs.fr/biom/soft–cr.

CITES, 1999. Identification manual for the white shark, *Carcharodon carcharias* Linnaeus. 1–14.

Clarke, S., Milner–Gulland, E., and Bjorndal, T. 2007. Social, economic and regulatory drivers of the shark fin trade. Marine Resource Economics, 22: 305–327.

Clavel, J., Robert, A., Devictor, V., Julliard, R. 2008. Abundance estimation with a transient model under the robust design. The Journal of Wildlife Management, 72(5): 1203–1210.

Cliff, G., Dudley, S., and Davis, B. 1989. Sharks caught in the protective gill nets off Natal, South Africa. 2. The great white shark *Carcharodon carcharias* (Linnaeus). South African Journal of Marine Science, 8: 131–144.

Cliff, G., Dudley, S., and Jury, M. 1996a. Catches of white sharks in KwaZulu–Natal, South Africa, and environmental influences. In: Klimley, P., and Ainley, D. (Eds). Great white sharks. The biology of *Carcharodon carcharias*: Pp 351–362.

Cliff, G., Van der Elst, R., Govender, A., Witthuhn, T., and Bullen, E. 1996b.First estimates of mortality and population size of white sharks on the South African coast. In: Klimley, P., and Ainley, D. (Eds). Great white sharks. The biology of *Carcharodon carcharias*: Pp 393–400.

Cliff, G., Compagno, L., Smale, M., Van Der Elst, R., and Wintner, S. 2000.First records of white sharks, *Carcharodon carcharias* from Mauritius, Zanzibar, Madagascar and Kenya. South African Journal of Science, 96: 365–367.

Cliff, G., Dudley, S., Ryan, P., and Singleton, N. 2002.Large sharks and plastic debris in KwaZulu-Natal, South Africa. Marine and Freshwater Research, 53: 575–581.

Clua, E., and Seret, B. 2012. New Caledonia (South Pacific) as a potential tropical wintering ground for the white shark, *Carcharodon carcharias*. In: Global perspectives on the biology and life history of the white shark (Ed. Domeier, M), 343–353. CRC Press, Boca Raton, Florida.

Coakes, A., Gowans, S., Simard, P., Giard, J., Vashro, C., and Sears, R. 2005. Photographic identification of fin whales (*Balaenoptera physalus*) of the Atlantic coast of Nova Scotia, Canada. Marine Mammal Science, 21 (2): 323–326.

Compagno, L. 1991. Government protection for the great white shark (*Carcharodon carcharias*) in South Africa. South African Journal of Marine Science, 87: 284–285.

Compagno, L. 2001. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Vol. 2: Bullhead, mackerel and carpet sharks (Heterodontiformes,

Lamniformes and Orectolobiformes).FAO species catalogue for fishery purposes. No 1, Vol. 2. Rome, FAO. 2001. Pp: 269.

Compagno, L., Marks, M., and Fergusson, I. 1997. Threatened fishes of the world, *Carcharodon carcharias*. Environmental Biology of Fishes, 50: 61–62.

Cooch, E., and White, G. (n.d.). Program MARK - A Gentle Introduction. MARK.

Cormack, R. 1964.Estimates of survival from the sighting of marked animals. Biometrika, 5: 429–438.

Davies, D. 1964.About sharks and shark attack. Shutter and Shooter: Pietermaritzburg, South Africa.

Dewar, H., Domeier, M., and Nasby-Lucas, N. 2004.Insights into young of the year white shark, *Carcharodoncarcharias*, behaviour in the Southern California Bight. Environmental Biology of Fishes, 70: 133–143.

De Vos, A. 2010. Anti-predator behaviour by cape fur seals *Arctocephalus pusillus pusillus* in relation to predation by white sharks *Carcharodon carcharias* around Seal Island, False Bay. PhD Thesis. Zoology Department, University of Cape Town.

Dicken, M. 2008.First observations of young of the year and juvenile great white sharks (*Carcharodon carcharias*) scavenging from a whale carcass. Marine and Freshwater Research, 59: 596–602.

Dicken, M., Smale, M., and Booth, A. 2006. Spatial and seasonal distribution patterns of the ragged–tooth shark *Carcharias taurus* along the coast of South Africa. African Journal of Marine Science, 28: 603–616.

Dicken, M., Smale, M., and Booth, A. 2013. White sharks *Carcharodon carcharias* at Bird Island, South Africa. African Journal of Marine Science.

Domeier, M. 2012. A new life–history hypothesis for white sharks, *Carcharodon carcharias*, in the Northeast Pacific. In: Global perspectives on the biology and life history of the white shark (Ed. Domeier, M), 199–223. CRC Press, Boca Raton, Florida.

Domeier, M., and Nasby–Lucas, N. 2007. Annual re-sightings of photographically identified white sharks (*Carcharodon carcharias*) at an eastern Pacific aggregation site (Guadalupe Island, Mexico).Marine Biology, 150: 977–984.

Domeier, M., and Nasby–Lucas, N. 2008. Migration patterns of white sharks (*Carcharodon carcharias*) tagged at Guadalupe Island, Mexico, and identification of an eastern Pacific shared offshore foraging area. Marine Ecology Progress Series, 370: 221–237.

Domeier, M., and Nasby–Lucas, N. 2012.Sex–specific migration patterns and sexual segregation of adult white sharks, *Carcharodon carcharias*, in the north-eastern Pacific. In: Global perspectives on the biology and life history of the white shark (Ed. Domeier, M), 133–146. CRC Press, Boca Raton, Florida.

Dudgeon, C., Noad, M., and Lanyon, J. 2008. Abundance and demography of a seasonal aggregation of zebra sharks *Stegostoma fasciatum*. Marine Ecology Progress Series, 368: 269–281.

Dudley, S. 1997. A comparison of the shark control programs of New South Wales and Queensland (Australia) and KwaZulu–Natal (South Africa).Ocean and Coastal Management, 34(1): 1–27.

Dudley, S. 2012. A review of research on the white shark, *Carcharodon carcharias*, in southern Africa. In: Global perspectives on the biology and life history of the white shark (Ed. Domeier, M), 511–533. CRC Press, Boca Raton, Florida.

Dudley, S., and Simpfendorfer, C. 2006. Population status of 14 shark species caught in the protective gillnets off KwaZulu–Natal beaches, South Africa, 1978–2003. *Marine and Freshwater Research*, *57*(2), 225–240. doi: 10.1071/MF05156.

Dudley, S., and Cliff, G. 2010. Influence of the annual sardine run on catches of large sharks in the protective gillnets off KwaZulu-Natal, South Africa, and the occurrence of sardine in shark diet. African Journal of Marine Science, 32(2): 383–397. doi:10.2989/1814232X.2010.502641.

Dudley, S., Anderson–Reade, M., Thompson, G., and McMullen, P. 2000. Concurrent scavenging off a whale carcass by great white sharks, *Carcharodon carcharias*, and tiger sharks. Fisheries Bulletin, 98: 646–649.

Dulvy, N., Baum, J., Clarke, S., Compagno, L., Cortes, E., Domingo, A., Fordham, S., Fowler, S., Francis, M., Gibson, C., Martinez, J., Musick, J., Stevens, J., and Valenti, S. 2008. You can swim but you can't hide: the global status and conservation of oceanic pelagic sharks and rays. Aquatic Conservation: Marine and Freshwater Ecosystems. doi: 10.1002/aqc.975.

Du Plessis, A., and Glass, J. 1991. The geology of False Bay. Transactions of the Royal Society of South Africa, 47: 495e517.

Estes, J., Terborgh, J., Brashares, J., Power, M., Berger, J., Bond, W., Carpenter, S., Essington, T., Holt, R., Jackson, J., Marquis, R., Oksanen, L., Oksanen, T., Paine, R., Pikitch, E., Ripple, W., Sandin, S., Scheffer, M., Schoener, T., Shurin, J., Sinclair, A., Soulé, M., Virtanen, R., and Wardle, D. 2011. Trophic downgrading of planet earth. Science, 333: 301–306.

Estrada, J., Rice, A., Natanson, N., and Skomal, G. 2006. Use of isotopic analysis of vertebrae in reconstructing ontogenetic feeding ecology in white sharks. Ecology, 87: 829–834.

Fergusson, I. 1996. Distribution and autoecology of the white shark in the eastern North Atlantic Ocean and the Mediterranean Sea. In: Klimley, P., and Ainley, D. (Eds). Great white sharks, the biology of *Carcharodon carcharias*: Pp 321–345.

Ferreira, C., and Ferreira, T. 1996.Population dynamics of white sharks in South Africa. In: Klimley, P. and Ainley, D. (Eds). Great white sharks. The biology of *Carcharodon carcharias*: Pp 381–391.

Food and Agriculture Organisation of the United Nations. 1999. International plan of action for the conservation and management of sharks. In: FAO Fisheries and Aquaculture Department [online]. Rome. [Cited 8 November 2011]. http://www.fao.org/fishery/ipoa–sharks/en, IPAO–Sharks, FAO 1999.

Food and Agriculture Organisation of the United Nations. 2004. Report of the FAO expert advisory panel for the assessment of proposals to amend appendices I and II of CITES concerning commercially–exploited aquatic species. FAO Fisheries Reports, 748: 01–51.

Francis, M. 1996.Observations on a pregnant white shark with a review of reproductive biology. In: Klimley, P., and Ainley, D. (Eds). Great white sharks. The biology of *Carcharodon carcharias*: Pp 157–172.

Gadig, O., and Rosa, R. 1996.Occurrence of the white shark along the Brazilian coast. In: Klimley, P., and Ainley, D. (Eds). Great White Sharks: The Biology of *Carcharodon carcharias*: Pp 347–350.

Gamble, L., Ravela, S., and McGarigal, K. 2008. Multi-scale features for identifying individuals in large biological databases: an application of pattern recognition technology to the marbled salamander *Ambystoma opacum*. Journal of Applied Ecology, 45: 170–180.doi:10.1111/j.1365–2664.2007.01368.

Gilkinson, A., Pearson, H., Weltz, F., and Davis, R. 2007.Photo-identification of sea otters using nose scars. Journal of Wildlife Management, 71(6): 2045–2051.doi:10.2193/2006–410.

Graham, R., and Roberts, C. 2007. Assessing the size, growth rate and structure of a seasonal population of whale sharks (*Rhincodon typus* Smith 1828) using conventional tagging and photo identification. Fisheries Research, 84: 71–80.

Grundlingh, M., and Largier, J. 1991. Physical oceanography of False Bay: a review. Transactions of the Royal Society of South Africa, 47(4–5): 387–400.

Gubili, C., Johnson, R., Gennari, E., Oosthuizen, H., Kotze, D., Meyer, M., Sims, D., Jones, C., and Noble, L. 2009. Concordance of genetic and fin photo identification in the great white shark, *Carcharodon carcharias*, off Mossel Bay, South Africa. Marine Biology, 156: 2199–2207.

Gubili, C., Duffy, C., Cliff, G., Wintner, S., Shivji, M., Chapman, D., Bruce, B., Martin, A., Sims, D., Jones, C., and Noble, L. 2012.Application of molecular genetics for conservation of the

white shark, *Carcharodon carcharias*, L. 1758. In: Global perspectives on the biology and life history of the white shark (Ed. Domeier, M), 357–380. CRC Press, Boca Raton, Florida.

Hammerschlag, N., Martin, R., and Fallows, C. 2006. Effects of environmental conditions on predator-prey interactions between white sharks (*Carcharodon carcharias*) and Cape fur seals (*Arctocephalus pusillus pusillus*) at Seal Island, South Africa. Environmental Biology of Fishes, 76: 341–350.

Heithaus, M. 2004. Predator-prey interactions. In: Biology of sharks and their relatives, Carrier, J., Musick, J., and Heithaus, M. (Eds). Boca Raton, FL: CRC Press. Pp 487–522.

Heithaus, M., Dill, L., Marshall, G., and Buhleier, B. 2002.Habitat use and foraging behaviour of tiger sharks (*Galeocerdo cuvier*) in a seagrass ecosystem. Marine Biology, 140: 237–248.

Heithaus, M., Frid, A., Wirsing, A., and Worm, B. 2008. Predicting ecological consequences of marine top predator declines. Trends in Ecology and Evolution, 23: 202–210.

Hestbeck, J. B., Nichols, J. D., and Malecki, R. 1991. Estimates of movement and site fidelity using mark-resight data of wintering Canada Geese. Ecology, 72: 523–533.

Holmberg, J., Norman, B., and Arzoumanian, Z. 2009. Estimating population size, structure, and residency time for whale sharks *Rhincodon typus* through collaborative photo–identification. Endangered Species Research, 7: 39–53. doi: 10.3354/esr00186.

Hurvich, C., and Tsai, C. 1989. Regression and time series model selection in small samples. Biometrika, 76: 297–307.

Hussey, N., McCann, H., Cliff, G., Dudley, S., Wintner, S., and Fisk, A. 2012.Size-based analysis of diet and trophic position of the white shark (*Carcharodon carcharias*) in South African waters. In: Global perspectives on the biology and life history of the white shark (Ed. Domeier, M), 27–50. CRC Press, Boca Raton, Florida.

IUCN. 1998. Shark Specialist Group (1998) Shark News: Newsletter of the IUCN Shark Specialist Group.

IUCN. 2011. IUCN Red List of Threatened Species. Version 2011.1. See www.iucnredlist.org. (date accessed 08 November 2011).IUCN (2011) Category A2cd+3cd ver. 3.1.

Jewell, O., Wcisel, M., Gennari, E., Towner, A., Johnson, R., and Singh, S. 2011. Effects of smart position only (SPOT) tag deployment on white sharks *Carcharodon carcharias* in South Africa. PLoSONE, 6(11): 4–7.doi:10.1371/journal.pone.0027242.

Jewell, O., Johnson, R., Gennari, E., and Bester, M. 2013.Fine scale movements and activity areas of white sharks (*Carcharodon carcharias*) in Mossel Bay, South Africa. Environmental Biology of Fishes. DOI 10.1007/s10641-012-0084-4.

Johnson, R. 2003.Behavioural ecology of the white shark (*Carcharodon carcharias*) at Dyer Island, South Africa. Masters Dissertation. University of Pretoria, South Africa.

Jolly, G. 1965. Explicit estimates from capture recapture data with both death and immigration-stochastic model. Biometrika, 52: 225 247.

Jorgensen, S., Reeb, C., Chapple, T., Anderson, S., Perle, C., Van Sommeran, S., Fritz–Cope, C., Brown, A., Klimley, P., and Block, B. 2010. Philopatry and migration of Pacific white sharks. Proceedings of the Royal Society B, 277: 679–688.doi:10.1098/rspb.2009.1155.

Jorgensen, S., Arnoldi, N., Estess, E., Chapple, T., and Rückert M. 2012.Eating or meeting? Cluster analysis reveals intricacies of white shark (*Carcharodon carcharias*) migration and offshore behaviour. PLoS ONE, 7(10): e47819. doi:10.1371/journal.pone.0047819.

Karczmarski, L., and Cockcroft, V. 1998. Matrix photo-identification technique applied in studies of free-ranging bottlenose and humpback dolphins. Aquatic Mammals, 24 (3): 143–147.

Kelly, M. 2001. Computer-aided photograph matching in studies using individual identification: an example from Serengeti cheetahs. Journal of Mammology, 82 (2): 440–449.

Kelly, J., and Klimley, P. 2003. Occurrence of the white shark, *Carcharodon carcharias*, at the Point Reyes Headlands, California. Fish and Game, 89(4): 187–196.

Kendall, W., and Bjorkland, R. 2001. Using open robust design models to estimate temporary emigration from capture-recapture data. Biometrics, 57(4): 1113–1122.

Kendall, W., and Nichols, J. 1995.On the use of secondary capture-recapture samples to estimate temporary emigration and breeding proportions. Journal of Applied Statistics, 22: 751–762.

Kendall, W., Nichols, J., and Hines, J. 1997. Estimating temporary emigration using capture-recapture data with Pollock's robust design. Ecology, 78: 563–578.

Kime, D., and Hews, E. 1982. The effect of temperature on steroid biosynthesis by testes of the dogfish, *Scyliorhinus caniculus*. Comparative Biochemistry and Physiology. Biochemistry and Molecular Biology, 71(4): 675–679.

Kirkman, S., Oosthuizen, H., and Meyer, M. 2006.The seal population of Seal Island, False Bay. In: Finding a balance: white shark conservation and recreational safety in the inshore waters of Cape Town, South Africa. Proceedings of a Specialist Workshop. WWF South Africa Report Series – 2006/Marine/001: 83–94. Nell, D., and Peschak, T. (Eds). Cape Town, WWF South Africa.

Kitchen–Wheeler, A. 2010.Visual identification of individual manta ray (*Manta alfredi*) in the Maldives Islands, Western Indian Ocean. Marine Biological Research.doi:10.1080/17451000903233763.

Klimley, P. 1985. The areal distribution and autoecology of the white shark, *Carcharodon carcharias*, off the west coast of North America. Memoirs of the Southern California Academy of Sciences, 9: 15–40.

Klimley, P. 1985b. Schooling in *Sphyrna lewini*, a species with low risk of predation: a non–egalitarian state. Ethology, 70(4): 297–319.

Klimley, P., Anderson, S., Pyle, P., and Henderson, R. 1992. Spatiotemporal patterns of white shark (*Carcharodon carcharias*) predation at the South Farallon Islands, California. Copeia, 3: 680–690.

Klimley, P., and Anderson, S. 1996. Residency patterns of white sharks at the South Farallon Islands, California. In: Klimley, P., and Ainley, D. (Eds). Great white sharks. The biology of *Carcharodon carcharias*: Pp 365–373.

Kock, A. 2002.Predatory activity of great white sharks (*Carcharodon carcharias*) around a Cape fur seal colony. Honours Thesis. University of Cape Town, Percy-Fitzpatrick Institute.

Kock, A., and Johnson, R. 2006. White shark abundance: Not a causative factor in numbers of shark bite incidences. In: Nel, D., and Peschak, T. (Eds). Finding a balance: White shark conservation and recreational safety in inshore waters of Cape Town, South Africa: Proceedings of a specialist workshop. WWF South Africa report series – 2006/Marine/001, Pp 1–19.

Kock, A., O'Riain, J., Mauff, K., Meÿer, M., Kotze, D., and Griffiths, C. 2013.Residency, habitat use and sexual segregation of white sharks, *Carcharodon carcharias* in False Bay, South Africa. PLoS ONE, 8(1): e55048. doi:10.1371/journal.pone.0055048.

Kohler, N., and Turner, P. 2001. Shark tagging: a review of conventional methods and studies. Environmental Biology of Fishes 60: 191–223.

Lamberth, S. 2006. White shark and other chondrichthyan interactions with the beach-seine (treknet) fishery in False Bay, South Africa. African Journal of Marine Science, 37–41.

Langtimm, C., Beck, C., Edwards, H., Fick-Child, K., Ackerman, B., Barton, S., and Hartley, W. 2004. Survival estimates for Florida manatees from the photo-identification of individuals. Marine Mammal Science, 20(3): 438–463.

Lindberg, M., and Rexstad, E. 2002. Capture–recapture sampling designs. Encyclopaedia of Environmetrics.1: 251-261.

Laroche, K., Kock, A., Dill, M., and Oosthuizen, H. 2007.Effects of provisioning ecotourism activity on the behaviour of white sharks, *Carcharodon carcharias*. Marine Ecology Progress Series, 338: 199–209.

Laroche, K., Kock, A., Dill, M., and Oosthuizen, H. 2008. Running the gauntlet: a predator-prey game between sharks and two age classes of seals. Animal Behaviour, 76: 1901–1917.

Last, P., and Stevens, J. 2009. Sharks and rays of Australia. CSIRO, Melbourne, Pp 478–480.

Letting, M., and Armstrong, D. 2003. An introduction to using mark-recapture analysis for monitoring threatened species. Department of Conservation Technical Series, New Zealand, 28(A): 5–32.

Lindberg, M. 2010.A review of designs for capture-mark-recapture studies in discrete time. Journal of Ornithology.doi:10.1007/s10336–010–0533–9.

Mace, G., *et al*. 2005. Biodiversity. Millennium Ecosystem Assessment: current state and trends: findings of the Condition and Trends Working Group. Ecosystems and human well-being. Vol. 1. Island Press, Washington, D.C.

Malcolm, H., Bruce, B., and Stevens, J. 2001. A review of the biology and status of white sharks in Australian waters. CSIRO Marine Research: Hobart, Tasmania.

Marshall, A., and Pierce, S. 2012. The use and abuse of photographic identification in sharks and rays. Journal of Fish Biology.80: 1361-1379.

Marshall, A., Dudgeon, C., and Bennett, M. 2011.Size and structure of a photographically identified population of manta rays *Manta alfredi* in southern Mozambique. Marine Biology, 158: 1111–1124.

Martin, R., Hammerschlag, N., Collier, R. and Fallows, C. 2005. Predatory behaviour of white sharks (*Carcharodon carcharias*) at Seal Island, South Africa. Journal of Marine Biological Association of the UK, 85: 1121–1135.

Maunder, M., Sibert, J., Fonteneau, A., Hampton, J., Kleiber, P., and Harley, S. 2006. Interpreting catch per unit effort data to assess the status of individual stocks and communities. ICES Journal of Marine Science, 63: 1373–1385.

Meekan, M., Bradshaw, C., Press, M., McLean, C., Richards, A., Quasnichka, S., and Taylor, J. 2006. Population size and structure of whale sharks *Rhincodon typus* at Ningaloo Reef, Western Australia. Marine Ecology Progress Series, 319: 275–285.

Mizroch, S., Herman, L., Straley, J., Glockner-Ferrari, D., Jurasz, C., Darling, J., Cerchio, S., Gabriele, C., Salden, D., and Von Ziegesar, O. 2004. Estimating the adult survival rate of central north Pacific humpback whales (*Megaptera novaeangliae*). Journal of Mammalogy, 85(5): 963–972.

Myers, R., Baum, J., Shepherd, T., Powers, S., and Peterson, C. 2007. Cascading effects of the loss of apex predatory sharks from a coastal ocean. Science, 315: 1846–1850.

Nasby–Lucas, N., and Domeier, M. 2012.Use of photo identification to describe a white shark aggregation at Guadalupe Island, Mexico. In: Global perspectives on the biology and life history of the white shark (Ed. Domeier, M), 381–392. CRC Press, Boca Raton, Florida.

Nasby–Lucas, N., Dewar, H., Lam, C., Goldman, K., and Domeier, M. 2009. White shark offshore habitat: A behavioural and environmental characterization of the Eastern Pacific shared offshore foraging area. PLoS ONE, 4(12): e8163.

Nelson, D., and Gruber, S. 1963. Sharks: Attraction by low–frequency sounds. Science, 142(3594): 975–977.doi:10.1126/science.142.3594.975.

Nichols, J., Hines, J., and Pollock, K. 1984a. Effects of permanent trap response in capture probability on Jolly–Seber capture-recapture model estimates. Journal of Wildlife Management, 48: 289–294.

Otis, D., Burnham, K., White, G., and Anderson, D. 1978. Statistical inference from capture data on closed animal populations. Wildlife Monographs, 62: 1-135.

Pardini, A., Jones, C., Noble, L., Kreiser, B., Malcolm, H., Bruce, B., Stevens, J., Cliff, G., Scholl, M., Francis, M., Duffy, C., and Martin, A. 2001. Sex biased dispersal of great white sharks. Nature, 412: 139–140.

Pepperell, J. 1992. Trends in the distribution, species composition and size of sharks caught by gamefish anglers off South–eastern Australia, 1961-1990.Australian Journal of Marine and Freshwater Research, 43: 213–225.

Pine, W., Pollock, K., Hightower, J., Kwak, T., and Rice, J. 2003. A review of tagging methods for estimating fish population size and components of mortality. Fisheries, 28: 10–23.

Pollock, K., Nichols, J., Brownie, C., and Hines, J. 1990.Statistical inference for capture-recapture experiments. Wildlife Monograph, 107: 1–97.

Porcher, I. 2005.On the gestation period of the blackfin reef shark, *Carcharhinus melanopterus*, in waters off Moorea, French Polynesia. Marine Biology, 146: 1207–1211.

Pradel, R. 1993. Flexibility in survival analysis from recapture data: Handling trap-dependence. In: Lebreton, J., and North, P. (Eds). Marked individuals in the study of bird population. Birkha Verlag, Basel, Switzerland. Pp 29–37.

Pradel, R., Hines, J., Lebreton, J., and Nichols, J. 1997. Capture-recapture survival models taking into account of transients. Biometrics, 53: 60–72.

Pratt, H. 1979. Reproduction in the blue shark, *Prionacea glauca*. Fisheries Bulletin, 77: 445–469.

Pratt, H. 1996. Reproduction in the male white shark. In: Klimley, P., and Ainley, D. (Eds). Great white sharks. The biology of *Carcharodon carcharias*: Pp 131–138.

Presser, J., and Allen, R. 1995.Management of the white shark in South Australia. SA Fisheries Management Series, Paper 6, May 1995. Primary Industries, South Australian Department of Fisheries, Adelaide.

Pyle, P., Anderson, S., and Ainley, D. 1996.Trends in white shark predation at the South Farallon Islands, 1968–1993. In Klimley, P., and Ainley, D. (Eds). Great White Sharks. The Biology of *Carcharodon carcharias*: Pp 375–380.

Reid, D., and Krogh, M. 1992. Assessment of catches from protective shark meshing off New South Wales beaches between 1950 and 1990. Australian Journal of Marine and Freshwater Research, 43: 283–296.

Riley, M., Hale, M., Harman, A., and Rees, R. 2010.Analysis of whale shark *Rhincodon typus* aggregations near South Ari Atoll, Maldives Archipelago. Aquatic Biology, 8: 145–150.

Robbins, R., and Booth, D. 2012. Seasonal, sexual and size segregation of white sharks *Carcharodon carcharias* at the Neptune Islands, South Australia. In: Global perspectives on the biology and life history of the white shark (Ed. Domeier, M), 287–299. CRC Press, Boca Raton, Florida.

Rogers, S., Church, D., Weatherly, A., and Pincock, D. 1984.An automated ultrasonic telemetry system for the assessment of locomotor activity in free-ranging trout, *Salmo gairdneri* Richerdson. Journal of Fish Biology, 25: 697–710.

Rose, D. 1996. An overview of world trade in sharks and other cartilaginous fishes TRAFFIC Network, Cambridge, UK.

Rowat, D., Speed, C., Meekan, M., Gore, M., and Bradshaw, C. 2009. Population abundance and apparent survival estimates of the Seychelles whale shark aggregation. Oryx, 43: 591–598.

Ryklief, R. 2012.Population dynamics of the white shark, *Carcharodon carcharias*, at Mossel Bay South Africa. Masters Dissertation. Nelson Mandela Metropolitan University, Port Elizabeth.

Sandercock, B. 2006. Estimation of demographic parameters from live–encounter data: A summary review. The Journal of Wildlife Management, 70(6): 1504–1520.

Schumann, E., Cohen, A., and Jury, M. 1996. Wind driven coastal SST along the south coast of South Africa and relationships to regional and global climate. Journal of Marine Research, 53: 231–248.

Schwarz, C., and Arnason, N. 1996. A general methodology for the analysis of open-model capture-recapture experiments. Biometrics, 52: 860–873.

Schwarz, C., and Seber, G. 1999. Estimating animal abundance: Review III. Statistical Science, 14(4): 427–456.

Schwarz, C., and Stobo, W. 1997. Estimating temporary migration using the robust design. Biometrics, 53:178–194.

Seber, G. 1965. A note on the multiple recapture census. Biometrika, 52: 249–259.

Seber, G. 1970. Estimating age-specific survival and reporting rates for adult birds from band returns. Biometrika, 57: 313–318.

Seber, G. 1982.The estimation of animal abundance and related parameters, 2nd Ed. Charles Griffin, London.

Semmens, J., Payne, N., Huveneers, C., Sims, D., and Bruce, B. 2013. Feeding requirements of white sharks may be higher than originally thought. Scientific Reports, 3: 1471. doi: 10.1038/srep01471.

Shivjy, M., Chapman, D., Pikitch, E., and Raymond, P. 2005. Genetic profiling reveals illegal international trade in fins of the great white shark, *Carcharodon carcharias*. Conservation Genetics, 6: 1035–1039.

Sims, D., Speedie, C., and Fox, A. 2000. Movements and growth of a female basking shark re-sighted after a three year period. Journal of the Marine Biological Association of the U.K. 80: 1141–1142.

Skomal, G., Chrisholm, J., and Correira, S. 2012. Implications of increasing pinniped interactions on the diet and abundance of white sharks off the coast of Massachusetts. In: Global perspectives on the biology and life history of the white shark (Ed. Domeier, M), 405–417. CRC Press, Boca Raton, Florida.

Smale, M., and Cliff, G. 2012. White sharks and cephalopod prey: Indicators of habitat use? In: Global perspectives on the biology and life history of the white shark (Ed. Domeier, M), 51–57. CRC Press, Boca Raton, Florida.

Soldo, A., and Jardas, I. 2002. Occurrence of great white shark, *Carcharodon carcharias* (Linnaeus, 1758) and basking shark, *Cetorhinus maximus* (Gunnerus, 1165) in the Eastern Adriatic and their protection. Periodicum Biologorum, 104 (2): 195–201.

Sosa–Nishizaki, O., Morales–Bojórquez, E., Nasby–Lucas, N., Oñate–González, E., and Domeier, M. 2012. Problems with photo-identification as a method of estimating abundance of white sharks, *Carcharodon carcharias*. In: Global perspectives on the biology and life history of the white shark (Ed. Domeier, M), 393–404. CRC Press, Boca Raton, Florida.

Spargo, P. 1991. False Bay, South Africa: An historic and scientific overview. Transactions of the Royal Society of South Africa, 47: 363–375.

Speed, C., Meekan, M., and Bradshaw, C. 2007. Spot the match-wildlife photo-identification using information theory. Frontiers in Zoology, 4: 1184–1182.

Stanley, T., and Burnham, K. 1999.A closure test for time-specific capture-recapture data. Environmental and Ecological Statistics, 6(2): 197-209.

Stevens, J., Bonfil, R., Dulvy, N., and Walker, P. 2000. The effects of fishing on sharks, rays and chimaeras (chondrichthyans), and the implications for marine ecosystems. ICES Journal of Marine Science, 57: 476–494.

Stanley, R. 1995. DARWIN: Identifying dolphins from dorsal fin images. Senior Thesis, Eckerd College.

Strong, W., Murphy, R., Bruce, B., and Nelson, D. 1992. Movements and associated observations of bait–attracted white sharks, *Carcharodon carcharias*: A Preliminary Report. Australian Journal of Marine and Freshwater Research, 43: 13–22.

Strong, W., Bruce, B., Nelson, D., and Murphy, R. 1996.Population dynamics of white sharks in Spencer Gulf, South Australia. In: Klimley, P., and Ainley, D. (Eds). Great white sharks. The biology of *Carcharodon carcharias*: Pp 401–414.

Sugiura, N. 1978.'Further analysis of the data by Akaike's Information Criterion and the finite corrections'. Communications in Statistics, Theory and Methods, A7: 13–26.

Sundström, L., Gruber, S., Clermont, S., Correia, J, and de Marignac, J. 2001.Review of elasmobranch behavioural studies using ultrasonic telemetry with special reference to the lemon shark, *Negaprion brevirostris*, around Bimini Islands, Bahamas. Environmental Biology of Fishes, 60: 225–250.doi:10.1023/A:1007657505099.

Thaka, R., and Gentleman, R. 1996. A language for data analysis and graphics. Journal of Computational and Graphical Statistics, 5(3): 299-314.

Towner, A., Smale, M., and Jewell, O. 2012. Boat strike wound healing in *Carcharodon carcharias*. In: Global perspectives on the biology and life history of the white shark (Ed. Domeier, M), 77–81. CRC Press, Boca Raton, Florida.

Towner, A., Wcisel, M., Reisinger, R., Edwards, D., and Jewell, O. 2013. Gauging the threat: the first population estimate for white sharks in South Africa using photo identification and automated software. PLoS ONE 8(6): e66035. doi:10.1371/journal.pone.0066035.

Towner, A., Underhill, L., Jewell, O., and Smale, M. 2013.Environmental influences on the abundance and sexual composition of white sharks *Carcharodon carcharias* in Gansbaai, South Africa. PLoS ONE 8(8): e71197. doi:10.1371/journal.pone.0071197.

Tricas, T., and McCosker, J. 1984.Predatory behaviour of the white shark (*Carcharodon carcharias*), with notes on its biology. Proceedings of the California Academy of Sciences, 43: 221–238.

Vincent, C., Fedak, M., McConnell, B., Meynier, L., Saist–Jean, C., and Ridoux, V. 2005.Status and conservation of grey seal, *Halichoerus grypus*, in France. Biological Conservation, 126: 62–73.doi:10.1016/j.bio–con.2005.04.022.

Wallett, T. 1973.Analysis of shark meshing returns off the Natal coast. Masters Dissertation. University of Natal, Durban.

Wallett, T. 1978.Shark attack and treatment of victims in Southern African waters. Purnell and Sons, Cape Town. Pp 176.

Ward P., and Myers, R. 2005. Inferring the depth distribution of catchability for pelagic fishes and correcting for variations in the depth of longline fishing gear. Canadian Journal of Fisheries and Aquatic Sciences, 62: 1130–1142.

Weltz, K., Kock, A., Winker, H., Attwood, C., and Sikweyiya, M. 2013. The influence of environmental variables on the presence of white sharks, *Carcharodon carcharias* at two popular Cape Town bathing beaches: A generalized additive mixed model. PLoS ONE, 8(7): e68554. doi:10.1371/journal.pone.0068554.

Weng, K., Boustany, A., Pyle, P., Anderson, S., Brown, A., and Block, B. 2007a.Migration and habitat of white sharks (*Carcharodon carcharias*) in the eastern Pacific Ocean. Marine Biology, 152: 877–894.

Weng, K., O'Sullivan, B., Lowe, C., Winkler, C., Dewar, H., and Block, B. 2007b.Movements, behaviour and habitat preferences of juvenile white sharks *Carcharodon carcharias* in the eastern Pacific. Marine Ecology Progress Series, 338: 211–224.

White, G., and Burnham, K. 1999. Program MARK: Survival estimation from populations of marked animals. Bird Study, 46 (Supplement): 120–138.

White, G., Burnham, K., and Anderson, D. 1999. Advanced features of program MARK. International Wildlife Management Congress, 368–377.

Williams, B., Nichols, J., and Conroy, M. 2002. Analysis and management of animal populations: modelling, estimation, and decision making. Academic Press, San Diego, California.

Wilson, B., Hammond, P., and Thompson, P. 1999. Estimating size and assessing trends in a coastal bottlenose dolphin population. Ecological Applications, 9(1): 288–300.

Willson, J., Winne, C., and Todd, B. 2011. Ecological and methodological factors affecting detectability and population estimation in elusive species. Journal of Wildlife Management, 75: 36–45.

Wintner, S., and Cliff, G. 1999.Age and growth determination of the white shark, *Carcharodon carcharias*, from the east coast of South Africa. Fisheries Bulletin, 97(1): 153–169.

Worm, B., Davis, B., Kettemer, L., Ward-Paige, C., Chapman, D., Heithaus, M., Kessel, S., and Gruber, S. 2013.Global catches, exploitation rates, and rebuilding options for sharks. Marine Policy, 40: 194–204.doi:10.1016/j.marpol.2012.12.034.

Würsig, B., and Jefferson, T. 1990. Methods of photo-identification for small cetaceans. Reports of the International Whaling Commission (Special Issue), 12: 43–52.

Zehfuss, K., Hightower, J., and Pollock, K. 1999. Abundance of Gulf sturgeon in the Apalachicola River, Florida. Transactions of the American Fisheries Society, 128: 130–143.

Zoo, C. 2004. White Shark *Carcharodon carcharias*: status and management challenges. Conclusions of the Workshop on Great White Shark Conservation Research Wildlife Conservation Society. Population Trends, 1: 1–7.

Zuffa, M., Van Grevelynghe, G., De Maddalena, A., and Storai, T. 2002.Records of the white shark, *Carcharodon carcharias* (Linnaeus, 1758) from the Western Indian Ocean. South African Journal of Science, 98(7/8): 347–349.

APPENDIX A

Table A.1.Capture histories for 303 photo-identified male (n = 112), female (n = 111), and unsexed (n = 80) *C. carcharias* from Seal Island, South Africa.

Number	Ref. #	Sex	2004	2005	2006	2007	2008	2009	2010	2011	2012
1	WS0001	M									
2	WS0002	M									
3	WS0003	F									
4	WS0005	F									
5	WS0006	M									
6	WS0009	F									
7	WS0010	F									
8	WS0011	M									
9	WS0012	F									
10	WS0014	U									
11	WS0015	M									
12	WS0016	F									
13	WS0017	F									
14	WS0018	F									
15	WS0019	U									
16	WS0020	M									
17	WS0021	F									
18	WS0022	M									
19	WS0023	M									
20	WS0024	F									
21	WS0025	F									
22	WS0026	M									
23	WS0027	M									
24	WS0028	U									
25	WS0029	F									
26	WS0030	M									
27	WS0031	F									
28	WS0032	M									
29	WS0033	F									
30	WS0034	U									
31	WS0035	M									
32	WS0036	F									
33	WS0037	F									
34	WS0038	M									
35	WS0039	U									
36	WS0040	U									
37	WS0041	M									
38	WS0042	M									
39	WS0043	U									
40	WS0044	F									
41	WS0045	F									
42	WS0046	M									
43	WS0047	M									
44	WS0048	M									
45	WS0049	F									
46	WS0050	F									
47	WS0051	M									
48	WS0052	U									
49	WS0053	F									
50	WS0054	F									
51	WS0055	M									
52	WS0056	U									
53	WS0057	M									
54	WS0058	U									
55	WS0059	M									
56	WS0060	U									
57	WS0061	U									
58	WS0062	F									
59	WS0063	F									

Table A.1.Continued.

Number	Ref. #	Sex	2004	2005	2006	2007	2008	2009	2010	2011	2012
60	WS0064	F									
61	WS0065	F									
62	WS0066	U									
63	WS0067	F									
64	WS0068	F									
65	WS0069	M									
66	WS0070	U									
67	WS0071	F									
68	WS0072	F									
69	WS0073	F									
70	WS0074	M									
71	WS0075	F									
72	WS0077	U									
73	WS0078	F									
74	WS0079	F									
75	WS0080	M									
76	WS0081	F									
77	WS0083	M									
78	WS0084	M									
79	WS0086	U									
80	WS0089	M									
81	WS0090	M									
82	WS0091	M									
83	WS0092	M									
84	WS0094	M									
85	WS0095	F									
86	WS0096	F									
87	WS0097	F									
88	WS0098	M									
89	WS0099	U									
90	WS0100	U									
91	WS0101	F									
92	WS0102	M									
93	WS0103	M									
94	WS0104	M									
95	WS0105	M									
96	WS0106	M									
97	WS0107	M									
98	WS0108	U									
99	WS0109	F									
100	WS0110	M									
101	WS0111	U									
102	WS0112	M									
103	WS0115	F									
104	WS0116	M									
105	WS0117	F									
106	WS0118	F									
107	WS0119	M									
108	WS0120	F									
109	WS0121	F									
110	WS0122	F									
111	WS0123	U									
112	WS0124	F									
113	WS0125	M									
114	WS0126	F									
115	WS0127	M									
116	WS0128	M									
117	WS0129	M									
118	WS0130	M									
119	WS0131	F									
120	WS0132	M									
121	WS0134	M									
122	WS0135	F									
123	WS0136	U									
124	WS0137	F									

Table A.1.Continued.

Number	Ref. #	Sex	2004	2005	2006	2007	2008	2009	2010	2011	2012
125	WS0138	U									
126	WS0139	U									
127	WS0140	F									
128	WS0149	F									
129	WS0150	F									
130	WS0151	M									
131	WS0152	M									
132	WS0153	M									
133	WS0154	F									
134	WS0155	M									
135	WS0156	F									
136	WS0157	U									
137	WS0158	U									
138	WS0159	F									
139	WS0160	U									
140	WS0161	M									
141	WS0162	M									
142	WS0163	F									
143	WS0164	M									
144	WS0165	F									
145	WS0166	M									
146	WS0167	M									
147	WS0168	F									
148	WS0170	F									
149	WS0171	F									
150	WS0172	M									
151	WS0173	M									
152	WS0174	M									
153	WS0175	U									
154	WS0176	F									
155	WS0177	M									
156	WS0178	F									
157	WS0179	F									
158	WS0180	F									
159	WS0181	U									
160	WS0182	F									
161	WS0183	U									
162	WS0184	U									
163	WS0185	U									
164	WS0186	U									
165	WS0187	F									
166	WS0188	F									
167	WS0189	U									
168	WS0191	U									
169	WS0192	M									
170	WS0194	U									
171	WS0195	U									
172	WS0197	U									
173	WS0198	U									
174	WS0199	U									
175	WS0200	F									
176	WS0201	U									
177	WS0202	U									
178	WS0203	U									
179	WS0204	U									
180	WS0205	U									
181	WS0206	U									
182	WS0207	M									
183	WS0208	U									
184	WS0209	U									
185	WS0211	U									
186	WS0212	U									
187	WS0216	F									
188	WS0217	U									
189	WS0218	F									

Table A.1.Continued.

Number	Ref. #	Sex	2004	2005	2006	2007	2008	2009	2010	2011	2012
190	WS0219	M									
191	WS0220	U									
192	WS0221	F									
193	WS0222	F									
194	WS0223	F									
195	WS0224	F									
196	WS0226	F									
197	WS0227	M									
198	WS0228	M									
199	WS0230	M									
200	WS0231	F									
201	WS0232	M									
202	WS0233	M									
203	WS0234	U									
204	WS0236	F									
205	WS0238	M									
206	WS0239	M									
207	WS0240	U									
208	WS0242	U									
209	WS0243	U									
210	WS0244	U									
211	WS0245	U									
212	WS0246	F									
213	WS0247	M									
214	WS0248	M									
215	WS0250	F									
216	WS0251	F									
217	WS0252	U									
218	WS0253	U									
219	WS0254	F									
220	WS0255	U									
221	WS0256	U									
222	WS0257	M									
223	WS0258	M									
224	WS0259	M									
225	WS0260	U									
226	WS0261	U									
227	WS0262	M									
228	WS0263	U									
229	WS0264	F									
230	WS0265	M									
231	WS0266	U									
232	WS0268	F									
233	WS0269	F									
234	WS0270	F									
235	WS0272	F									
236	WS0274	F									
237	WS0275	M									
238	WS0276	U									
239	WS0278	U									
240	WS0280	U									
241	WS0291	U									
242	WS0300	F									
243	WS0301	F									
244	WS0302	U									
245	WS0303	F									
246	WS0304	M									
247	WS0305	F									
248	WS0306	M									
249	WS0307	F									
250	WS0308	F									
251	WS0309	M									
252	WS0311	U									
253	WS0312	F									
254	WS0314	U									

Table A.1.Continued.

Number	Ref. #	Sex	2004	2005	2006	2007	2008	2009	2010	2011	2012
255	WS0315	M									
256	WS0316	F									
257	WS0317	M									
258	WS0318	M									
259	WS0319	F									
260	WS0321	M									
261	WS0323	F									
262	WS0324	M									
263	WS0325	M									
264	WS0327	F									
265	WS0329	M									
266	WS0331	M									
267	WS0332	M									
268	WS0333	M									
269	WS0334	F									
270	WS0335	U									
271	WS0336	M									
272	WS0337	M									
273	WS0338	F									
274	WS0339	F									
275	WS0340	F									
276	WS0342	M									
277	WS0343	F									
278	WS0346	M									
279	WS0347	U									
280	WS0348	M									
281	WS0349	F									
282	WS0350	F									
283	WS0351	M									
284	WS0352	F									
285	WS0353	M									
286	WS0354	M									
287	WS0355	M									
288	WS0356	U									
289	WS0357	U									
290	WS0359	M									
291	WS0360	U									
292	WS0361	U									
293	WS0362	U									
294	WS0363	F									
295	WS0364	M									
296	WS0365	M									
297	WS0366	F									
298	WS0367	U									
299	WS0368	F									
300	WS0369	M									
301	WS0370	M									
302	WS0371	M									
303	WS0372	M									